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Robert Fogel

Forest Science Department
Oregon State University
Corvallis, Oregon 97331

and

James M. Trappe

Pacific Northwest Forest and Range Experiment Station
Forestry Sciences Laboratory
Corvallis, Oregon 97330

Fungus Consumption (Mycophagy) by Small Animals

Abstract

A review of the natural history literature of small mammal feeding habits, based on many fortuitous field observations, some analysis of stomach contents, and a few feeding experiments, shows that diverse animals feed on similarly diverse fungi. The interdependence of animals and fungi has evolved to a high degree in some cases, e.g., the loss of alternative spore dispersal mechanisms by some fungi and the strong reliance of some mammals on fungi as a primary food. Consequently, adaptation for mycophagy and the effects on mycophagy of habitat, fungal toxicity, and the food value of fungi have implications in the interpretation of ecosystem structure and function.

Introduction

Truffles and other hypogeous fungi occupy a highly specialized, protected niche as subterranean-fruiting symbionts with roots of higher plants. Such fungi depend on mammal and invertebrate mycophagy for spore dispersal. These and other fungi, in turn, are important in the diet of many animals and in some cases comprise the major food source.

These interrelationships between fungi and animals engender many questions relevant to the life histories and ecosystematic roles of both. For example, which animals depend largely on fungi for food, for water, or for vitamins? What are the behavioral implications of seeking, drying, and caching fungi? What food values do mycophagists derive from fungi? Can animals differentiate between poisonous and nonpoisonous fungi? What is the phylogenetic significance of the various fungal mechanisms evolved for attracting mycophagists? What role does mycophagy play in fungus dispersal? What impact does mycophagy have on food chain and ecosystem dynamics, and where need it be recognized in ecosystem modeling?

The following literature review is intended to aid and stimulate a search for answers to such questions with emphasis on mammals, although similar questions can be asked about other animals as well. Little comprehensive research has been done on animal mycophagy. To interpret scattered fragments of published information, we have filled some gaps with speculation in hope of fostering further research in this fascinating field. Our literature search led to compilation of the reciprocal lists of mammal mycophagists and fungi eaten, presented later in this paper. Authorities for all species mentioned in the text are given in these lists.

The Small Mammal as Mycophagist

Many fortuitous field observations, some analyses of mammal stomach contents, and

a few feeding experiments have revealed that diverse mammals feed on similarly diverse fungi. The mammals include insectivores, omnivores, herbivores, and carnivores. The fungi include saprophytes, symbionts, and parasites. The interdependence of animals and fungi has evolved to a high degree in some cases, e.g., the loss of alternative spore dispersal mechanisms by the phylogenetically advanced truffles and other subterranean-fruiting fungi (Bessey, 1935; Burnett, 1968; Christenson, 1951; Kavaler, 1965; Gäumann and Dodge, 1928; Ingold, 1953, 1961, 1966; Korf, 1973; Lilly and Burnett, 1951; Rolfe and Rolfe, 1925; Smith, 1938; Trappe, 1971) and the strong reliance of some mammals on fungi as a primary food.

The Sciuridae (chipmunks and squirrels) have been the most observed mammalian mycophagists; consequently, they are also reported to eat the greatest variety of fungi. *Tamiasciurus hudsonicus* (red squirrel) has been credited with eating 89 species of fungi, more than any other mycophagist. Other relatively small mycophagists include members of the Cricetidae (mice, rats, lemmings, voles), Zapodidae (jumping mice), Ochotonidae (pikas), Soricidae (shrews), Didelphidae (opossums), Peramelidae (bandicoots), Phascolomidae (wombats), Macropodidae (rat-kangaroos), Cynopithecinae (baboons), Dasypodidae (armadillos), Leporidae (rabbits and hares), Castoridae (beavers), and Mustelidae (weasels). The reports of fungi in stomachs of shrews may at least in part reflect predation on fungus-feeding invertebrates or other animals rather than mycophagy by the shrews themselves.

The relative importance of fungi in small mammal diets has been estimated as percent of yearly dietary volume for several species (Table 1).

TABLE 1. Yearly dietary volume of fungi (%) for nine small mammal species.

Species	Volume (%)	Source
Eutamias townsendii	72	Tevis, 1953
Eutamias quadrimaculatus	66	Tevis, 1953
Spermophilus lateralis	61	Tevis, 1953
Tamiasciurus douglasii	56	McKeever, 1964
Sciurus griseus	52	Steinecker and Browning, 1970
Eutamias speciosus	32	Tevis, 1953
Eutamias amoenus	27	Tevis, 1953
Clethrionomys glareolus	7	Drożdż, 1966
Apodemus flavicollis	1	Drożdż, 1966

Tevis (1953) suggested a direct correlation between mammal body weight and importance of fungi in the diet among the *Spermophilus* spp. and *Eutamias* spp. that he studied. Other factors of habit and habitat are undoubtedly as much or more causally related to mycophagy. However, a relationship between mammal size and size of fungus eaten does seem likely in the sense that very small fungal species appear to be eaten only by smaller mammals. For instance, sporocarps of many species of the phycomycetous family, Endogonaceae, are often less than a millimeter in diameter and rarely exceed a few millimeters. These species have been reported only in stomach contents of small mammals such as shrews, voles, mice, jumping mice, pikas, etc., but they eat larger fungi as well (Bakerspiegel, 1958; Calhoun, 1941; Hamilton, 1941a; Jameson, 1952; Whitaker, 1962, 1963a; Whitaker and Ferraro, 1963; Whitaker and Maser, 1976).

Adaptations for Mycophagy

Morphological adaptations of small mammals are probably directly related to mycophagy. Animals adapted for digging might be expected to have an advantage in the search for truffles and other hypogeous fungi. Species with weak teeth might be more impelled to eat fungi when available. Unfortunately, the data presently available are too scanty to test these hypotheses.

Mammalian food-gathering behavior has evolved for locating fungi. Tevis (1953) observed innumerable small pits left in the soil from extraction of hypogeous fungi by animals; indeed, mycologists have long used this sign to indicate when and where to seek such fungi. Small mammal mycophagists probably locate hypogeous fungi by odor. Most hypogeous fungi have a noticeable odor at maturity which is almost overwhelming to many humans (Parks, 1919). Often the presence of these fungi is not visible on the soil surface. The ability of squirrels to detect mast by odor has been reported many times (Allen, 1943; Cahalane, 1942; Cram, 1924; Dice, 1927; Ingles, 1947; Ognev, 1940). We have observed over years of extensive collecting of hypogeous fungi that sporocarp odor is not detectable on immature specimens. As some spores reach maturity, a light odor often can be noticed; as the proportion of mature spores increases, so does the intensity of odor. Thus the fungus may remain undetected at early stages of development but emits increasingly strong odors as it matures.

Bright color as well as odor may attract small mammals to epigeous mushrooms and puffballs (Ingles, 1947). Mushrooms are sometimes nibbled *in situ* but are also harvested whole. Numerous observers have reported mushrooms hung in tree branch forks by squirrels, at times the tree "appearing bedecked for Christmas," (Cram, 1924; Hatt, 1929; Krieger, 1967; Marie, 1927, Odell, 1925, 1926; Ognev, 1940; Stakhrovskii, 1932). Since dried fungi preserve indefinitely, the intent of the squirrels is presumably to dry them for caching. Hardy (1949) found a cache of sporocarps left by a *Tamiasciurus hudsonicus* in a hollow tree trunk.

Mycophagy and Habitat

The characteristics of plant communities to which small mammals have become adapted are decidedly related to mycophagy. Forests of ectomycorrhizal trees such as the Pinaceae, Fagaceae, or Betulaceae produce a greater abundance of relatively large, fleshy mushrooms and hypogeous fungi, the typical fruiting forms of ectomycorrhizal fungi (Trappe, 1962). Plant communities of vesicular-arbuscular (VA) mycorrhizal hosts such as the Cupressaceae, Aceraceae, or herbaceous plants of fields, meadows, and bogs form mycorrhizae with certain genera of the Endogonaceae, which fruit hypogeously as single spores or very small, compact sporocarps (Gerdemann and Trappe, 1974). Thus, adjacent habitat types may differ strikingly in form and biomass of sporocarps produced. The small mammals that inhabit ectomycorrhizal forests might be expected to feed more on macrofungi than inhabitants of VA-mycorrhizal meadows. Although adequate data are not available, it can be hypothesized that mycophagy in VA-mycorrhizal redwood or maple forests resembles that of meadows more closely than that of ectomycorrhizal pine or oak forests. If this hypothesis is true, the qualitative and quantitative relationships of small mammal populations between these various kinds of habitats might deserve a new look.

Estimated annual production of epigeous mushrooms is summarized for several forest types in Table 2. The data of Richardson (1970) provide the best of the estimates presented, because his estimates are based on nearly weekly visits to the study site over a period of five years. The other estimates are based on relatively scanty data.

TABLE 2. Estimated production of epigeous mushrooms per ha yr^{-1}.

Forest Type	Kg Dry Wt	Kilocalories	Source
Oak and Beech, Hungary	7-160	30,000-658,000*	Hering, 1966
Beech, near Vienna	18-170	77,400-731,000*	Hering, 1966
Beech, Poland	4-5	17,200-21,500	Drożdż, 1965
Oak on slate soil, England	12-95	53,600-407,600	Hering, 1966
Oak on limestone soil, England	3-37	12,900-158,700	Hering, 1966
Conifer, Scotland	16-30	68,600-128,700	Richardson, 1970
Conifer, xeric inland forest, Pacific Northwest, U.S.A.	3	11,200	Smith, C., 1965
Conifer, xeric inland forest, Pacific Northwest, U.S.A.	10-17*	41,200-115,800*	Cooke, 1955
Conifer, Finland	5-19	22,300-82,800	Richardson, 1970
Conifer, Sweden	180	772,200	Richardson, 1970

* Our calculation, assuming 6.4% dry wt and 4300 calories g^{-1} dry wt (cf. Table 3).

Many variables interact to account for the wide range of production estimates; two most obvious are temperature and moisture and their interaction (Smith, 1949). Consequently, each climatic region has a characteristic fruiting pattern (Bohus, 1973; Ceruti, Montacchini a[illegible]loyez, 1967; Endo, 1973; Fogel, 1976; Grainger, 1946; Wilkins and Harr[illegible]roduction will vary from year to year within a region, depending on weath[illegible].cats within a region will vary one from another in production, depending on [illegible] microclimate, and vegetation.

No biomass production studies of VA-mycorrhizal fungi have been reported. However, Kessler and Blank (1972) estimated that nearly 7 million minute sporocarps of Endogonaceae occurred per ha in soil of a Michigan forest dominated by the VA-mycorrhizal *Acer saccharum* Marsh. A substantial biomass may be inferred. Fogel (1976) estimated the production of hypogeous basidiomycete and ascomycete sporocarps in a Western Oregon Douglas-fir stand to range from 11,052 to 16,753 sporocarps ha^{-1} and 2.3 to 5.4 kg dry weight ha^{-1}.

The Food Value of Fungi

Fresh, fleshy fungi range from 70 to 94 percent water by weight; large volumes therefore must be eaten to provide adequate protein and phosphorus (Miller and Halls, 1969; Winton and Winton, 1935). The drying of mushrooms by squirrels concentrates their food value. At the same time, fresh fungi might be an important source of water for animals unable to exist on bound or metabolic water when free water is unavailable (Getz, 1968; C. Smith, 1965).

Some measures of the food value of fungi are compared with those of other food sources in Tables 3-5. The data should be interpreted only in a broad sense, since several sources and differing analytical methodologies are represented in the compilation. Fresh, fleshy fungi resemble fruits and vegetables in containing substantially fewer

calories gm^{-1} than fresh nut kernels, eggs, or meat (Table 3). On a dry-weight basis, fungi compare favorably with blueberries and mast but contain about a third fewer calories than conifer seed (Table 4). Compared to nut kernels, dried mushrooms are good sources of protein, carbohydrates, and minerals but not fats (Table 5).

The net caloric value of any food to a consumer is the total caloric content digested minus the calories expended in seeking, extracting, ingesting, digesting, and excreting

TABLE 3. Caloric value of fresh foods (kcal. gm^{-1} fresh wt.).

Food	Calories	Source
FUNGI		
Agaricus bisporus	0.3-0.5	Singer, 1951; Pilát and Ŭsak, 1958
Boletus sp.	0.3	Singer, 1951
Boletus edulis	0.3-0.7	Pilát and Ŭsak, 1958; Andreotti and Casoli, 1968
Lentinus edodes	0.3	Singer, 1951
Lactarius deliciosus	0.5	Singer, 1951; Pilát and Ŭsak, 1958
Tuber melanosporum	0.4-0.6	Andreotti and Casoli, 1968
"mushrooms"	0.1-0.5	Singer, 1951; Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
Mean	0.4	
NUTS		
pine kernels	6.3	Hodgman *et al.*, 1959
Beechnut kernels	6.3-7.0	Proudfit and Robinson, 1961
butternut kernels	7.1-7.4	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
chestnut kernels	7.5-7.6	Proudfit and Robinson, 1961
hazelnut kernels	6.7	Proudfit and Robinson, 1961
hickory nut kernels	1.9	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
pecan kernels	6.6	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
walnut kernels	6.7-7.0	Proudfit and Robinson, 1961
Mean	6.2	
FRUITS		
apples	0.6	Proudfit and Robinson, 1961
blackberries	0.6	Proudfit and Robinson, 1961
blueberries	0.7	Proudfit and Robinson, 1961
cherries	0.7	Proudfit and Robinson, 1961
currants	0.6	Proudfit and Robinson, 1961
plums	0.6	Proudfit and Robinson, 1961
strawberries	0.4	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
Mean	0.6	
VEGETABLES		
lettuce	0.2	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
onions	0.5	Proudfit and Robinson, 1961
water cress	0.2	Proudfit and Robinson, 1961
Mean	0.3	
EGGS and MEAT		
eggs	2.5	Proudfit and Robinson, 1961
beef	1.8-3.4	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
Mean	2.1	

the nondigested residual of that food. The relative value of fungal caloric sources for any mycophagist must be compared to other sources in terms of an energy budget. If less energy is expended per calorie gained in seeking and eating fungi than in seeds or insects, the relative value of fungi as an energy source is increased.

TABLE 4. Caloric value of dried plant parts (kcal. gm^{-1} dry wt.).

Food	Calories	Source
FUNGI		
Peridermium harknessii		
in *P. contorta* bark	5.0	Smith, C. 1965
Rhizopogon sp.	4.9	Smith, C. 1965
Russula decolorans		
gills and spores	4.8	Smith, C. 1965
pileal context	4.0	
stipe	4.2	
Suillus tomentosus		Smith, C. 1965
tubes and spores	5.2	
pileal context	4.2	
stipe	4.1	
Mean	4.5	
CONIFER SEEDS		
Abies amabilis	6.8	Smith, C. 1965
Abies lasiocarpa	7.1	Smith, C. 1965
Picea engelmanii	7.1	Smith, C. 1965
Picea excelsa	6.7	Danilov, 1938
Pinus contorta	6.8	Smith, C. 1965
Pinus silvestris	6.2	Danilov, 1938
Pinus monticola	7.4	Smith, C. 1965
Pinus ponderosa	7.6	Smith, C. 1965
Pinus pumila	6.9	Danilov, 1938
Pseudotsuga menziesii	7.1	Smith, C. 1965
Tsuga heterophylla	7.1	Smith, C. 1965
Mean	7.0	
MAST		
Acer saccharinum	4.2	Smith, C., 1970
Carya ovata	7.2	Smith, C., 1970
Juglans nigra	6.3	Smith, C., 1970
Quercus alba	4.0	Smith, C., 1970
Quercus macrocarpa	4.2	Smith, C., 1970
Quercus shumardii	5.3	Smith, C., 1970
Mean	5.2	
FRUIT		
Vaccinium deliciosum	5.3	Smith, C. 1965
BUDS		
Picea excelsa	4.0	Danilov, 1938

Unfortunately, the relative digestibility of different food sources is not known for different mammals. The large gastric caecum of many rodents has been suggested as a site of enzyme systems capable of extracting energy from β-linked carbohydrates of fungal cell walls (C. Smith, 1965). Our impression from examining stomach and fecal contents of several hundred small mammal mycophagists is that fungal cell cytoplasm is readily digested, cell walls are sometimes digested, and spores are not digested at

TABLE 5. Chemical composition of dried plant parts and meat.

Plant Species	% Dry Weight Protein	Fat	Carbohydrate	Ash	Source
FUNGI					
Agaricus bisporus	48-62	1-2	—	7	Singer, 1961
Amillaria mellea	16	—	76	8	Singer, 1961
Boletus edulis	32-35	5	58-59	6-8	Singer, 1961
Clavaria flava	19	2	47	5	Winton and Winton, 1935
Hygrophorus, Amillaria, Russula, Clitocybe, Amanita, Tricholoma, Pholiota sp.	12-27	—	—	—	Miller and Halls, 1969
Hygrophorus, Amanita sp.	23	—	—	—	Miller and Halls, 1969
Lactarius deliciosus	27	7	28	6	Singer, 1961
Lentinus edodes	19	5	54	3	Singer, 1961
Marasmius oreades	35-43	2-4	34	10	Singer, 1961
Morchella esculenta	34-35	2	46-47	9-11	Singer, 1961
Morchella sp.	30	—	—	—	Mendel, 1898
Morchella, Rhizopogon, Cortinarius, Lactarius Amanita, Clitocybe sp.	30	—	—	—	Miller and Halls, 1969
Pleurotus cretacius	21	—	—	—	Winton and Winton, 1935
Saccharomyces cerevisiae	12	<1	21	—	Hodgman, *et al.*, 1963
Suillus granulatus	14	2	70	6	Singer, 1961
Suillus grevillei	21	2	64	6	Singer, 1961
Suillus luteus	20	4	53	6	Singer, 1961
Tricholoma favovirens	15-18	—	71-78	7-11	Singer, 1961
Tuber melanosporum	25-26	2	39-46	8	Andreotti and Casoli, 1968
NUTS					
Chestnut kernels	11	7	72	2	Hodgman, *et al.*, 1963 Chapman and Baumgartner, 1939
Butternut kernels	28	61	3	3	Winton and Winton, 1932
Black walnut kernels	28-30	56-58	6	2	Winton and Winton, 1932 Chapman and Baumgartner, 1939
Pecan kernels	10-11	70-75	10	2	Winton and Winton, 1932
Hickory kernels	13-20	65-70	6-9	2	Winton and Winton, 1932
Filbert kernels	16-17	63-65	10-13	2	Winton and Winton, 1932
Beechnut kernels	22	42-57	19	3-4	Winton and Winton, 1932 Chapman and Baumgartner, 1939
MEAT					
Chipped beef	30	6	<1	—	Hodgman, *et al.*, 1963

all. Spores presumably contain concentrated energy sources, as indicated by the relatively high caloric values of gills or tubes of mushrooms as compared to the somatic parts (Table 4) and by the high lipid content seen in spores of some fungi (Gerdemann and Trappe, 1974). However, reports of squirrels eating caps and gills of mushrooms while leaving the stems (Hatt, 1929; Ognev, 1940; C. Smith, 1965) probably reflect palatability rather than selection for food value.

Aside from their caloric value, some of the diverse organic compounds of fungi may be important in small mammal physiology. For example, ergosterol, a possibly important source of mammalian hormone precursors, occurs widely in the higher fungi

and ranges from about 0.2 to 0.5 percent of the dry weight of fleshy fungi (Milazzo, 1965; Shivrina *et al.*, 1968; Catalfomo and Trappe, 1970). Fungi commonly contain other steroids, triterpenes, amines, indoles, and phenols (Catalfomo and Trappe, 1970) of unknown but potential use to mammals. Vitamins such as biotin, niacin, pantothenic acid, and riboflavin are produced in significant amounts by some fleshy fungi (Shemakhanova, 1967). On a fresh weight basis, mushrooms have higher concentrations of niacin and riboflavin than most nuts, fruits, and leaf vegetables and equal or excel most meats in this regard (Proudfit and Robinson, 1950).

Fungal tissues effectively accumulate nonmetallic and metallic elements. Stark (1972) found that sporocarps of five fungal species contained substantially higher concentrations of Cu, N, P, and Zn than did pine needles (dry wt. basis). At least some of the five also contained higher concentrations of Ca, Fe, K, Mg, and Na. Fungal rhizomorphs were also high in concentrations of these elements, e.g., 180 times as much Fe as pine needles.

The overall quality of fungi as a food source for small mammals has not been experimentally assessed. Tevis (1952) reported that *Eutamias* stomachs containing only fungi were always heavier than those of animals feeding on non-fungal material. He also found that when chipmunks began to acquire hibernation fat, those eating fungi became fat sooner. But Naumov's report of squirrels starving to death while gorged with *Polyporus betulinus* Fr. suggests that some fungi may have very little food value (Ognev, 1940), at least for some mammals.

Cyclic over-population of mammals and poor seed crops probably periodically enhance the importance of mycophagy in reducing food stress (Lampio, 1967; Ognev, 1940; Rajala and Lampio, 1963). The effect of poor mast crops, traditionally considered a key factor in regulating squirrel populations, might be moderated in good mushroom years (Baumgartner, 1939; Brown and Yeager, 1945; Stienecker and Browning, 1970; Uhlig, 1955; and others). Seasonal buildup of rodent populations, together with the seasonality of fungal fruiting, might explain the increased seasonal use of *Endogone* by *Peromyscus maniculatus, Microtus longicaudus, Clethrionomys gapperi, Phenacomys intermedius,* and *Zapus princeps* (Williams and Finney, 1964).

Fungal Toxins and Mycophagy

Feeding trials and field observations of *Amanita muscaria, Amanita phalloides, Lactarius rufus,* and *Lactarius torminosus* consumption by squirrels indicate that they and presumably other rodents can safely eat mushrooms considered poisonous to man (Ballou, 1927; Cram, 1924; Hastings and Mottram, 1916; Hatt, 1929; Klugh, 1927; Metcalf, 1925). With this evidence in mind, Walton's (1898) observation, "For thirteen years I have made use of the varieties of mushrooms selected by squirrels and wood mice as edible. . .," should be taken skeptically. He was lucky to have escaped poisoning.

We have found no reports on poisoning of small mammals by fungi in the wild. One prime reason may be that no one has seriously studied the matter. Several hypotheses might be proposed, among them that (A) no fungi are poisonous to small mammals; (B) mammals can detect toxins by taste, smell, or in some other way; or (C) mammals are poisoned by some fungi, but when poisoning occurs, they seclude themselves before symptoms become evident to observers.

Hypothesis A was supported by Ford (1908, 1910), who suggested that herbivore alimentary canals can neutralize poisons which are highly toxic if administered by subcutaneous or interperitoneal inoculation. However, chickens and a cow are reported to have died after eating sporocarps of *Amanita* sp. (Ballou, 1927). Recently it has been demonstrated that a number of toxins each with different properties are responsible for mushroom poisoning symptoms (Litten, 1975). The *Amanita* toxin phalloiden, for instance, is not toxic when given orally, but mice given *Amanita* whole toxic extract containing myriaphalloisins die in a few hours to four days.

Hypothesis B seems a reasonable possibility, considering the selective pressure against genetic lines given to feasting on poisonous fungi. Hypothesis C also seems reasonable, especially since most mycotoxins require some incubation time before symptoms are expressed: mushroom poisoning of humans often does not arouse symptoms for several hours after ingestion. Hypothesis A has been proven wrong for a limited number of mammals; B and C remain to be tested.

Mycophagists as Disseminators of Fungi

Mycophagy serves in fungal dissemination by physical transport of spores and hypothetically, at least in some cases, by breaking spore dormancy. Most epigeous fungi, even the coprophilous species, are adapted for aerial or water transport of spores; mycophagy would seem incidental to primary dispersal mechanisms (Ingold, 1953). Of course, mushrooms hung in trees by squirrels are exposed to air currents that could carry spores farther than those at the ground surface. Mycorrhizal species or root pathogens may gain some strategic advantage over aerial dissemination if spores are eaten and then excreted near susceptible host roots by burrowing mycophagists.

Hypogeous fungi, on the other hand, are clearly dependent on mycophagy for physical transport. They fruit underground, their spore-bearing tissues are typically enclosed in a persistent peridium, and for the most part they do not forcibly discharge their spores. Even those which can forcibly discharge spores, such as the truffle relative, *Geopora cooperi* Harkn. (Burdsall, 1965), must be dug up and opened above ground by an animal to release spores to air currents (Korf, 1973).

The phycomycetous fungi of the family Endogonaceae deserve special mention because they have been found so often in small rodent stomachs. The various species may be epigeous or hypogeous and may form sporocarps or be borne as individual spores in soil. At present, only the sporocarp-forming species have been found in rodent stomachs. Whether epigeous or hypogeous, the sporocarps are typically compact clusters of very large spores devoid of discharge mechanisms. Presumably, these sporocarps are strongly dependent on mycophagy for transport. Spores borne singly in soil, on the other hand, may be eaten by insects or arthropods but also can be transported by any of the forces that move soil (Gerdemann and Trappe, 1974).

The effects of passage through a digestive tract on spore germination are unknown for most fungi. In general, spores of coprophilous and xylophilous fungi germinate poorly or not at all under any circumstances (Fries, 1943; Benedict *et al.*, 1967). The relatively few reported successes in inducing germination of spores of ectomycorrhizal fungi entailed treatments such as low temperature, alternate wetting and drying, soil extracts, co-culture with other organisms, slug digestive enzymes, or exposure to living roots (Sussman and Halversen, 1966; Bowen and Theodorous, 1974; Lamb and Richards,

1974). Of the Endogonaceae, chlamydosporic species which form vesicular-arbuscular mycorrhizae germinate readily without special treatment; one species has been shown to be viable after passage through a *Microtus* digestive tract (Trappe and Maser, 1976). No one has yet succeeded in germinating spores of those that occur only in sporocarps, at least some of which are ectomycorrhizal species (Gerdemann and Trappe, 1974).

Mycophagy would subject ingested fungal spores to body heat, enzymatic action, and co-culture with the myriad microorganisms of digestive tracts and feces. The process has not been demonstrated to affect spore dormancy as yet. Indeed root exudates appear to induce germination of some hypogeous mycorrhizal fungi without mycophagy (Palenzona, 1969; Bowen and Theodorous, 1974). Since essentially no research has been reported on the physiological effects of mycophagy on spores, the question remains moot.

Mycophagy in Ecosystem Analysis

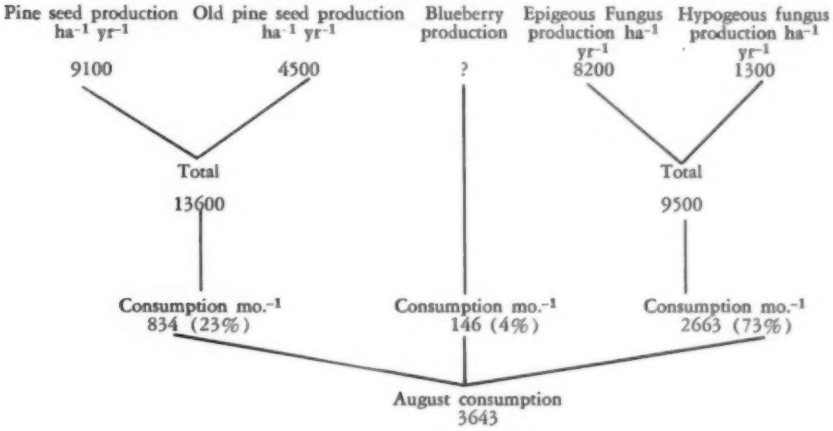
Invertebrates and vertebrates that feed wholly or in part on fungi have been arbitrarily categorized either as herbivores or fungal decomposers. No generalization fits comfortably, however, because the fungi may be saprophytes, biotrophic or necrotrophic symbionts, or predators (Harley, 1971; Lewis, 1973). Although necrotrophic symbionts may be considered "living tissue saprophytes" for purposes of ecosystem modeling, the biotrophic symbionts such as mycorrhizal fungi pose a special problem: the structural and physiological interdependence of fungus and host preclude their conceptual separation either physically or functionally.

One solution to this problem is to consider mycorrhizal fungi as extensions of the host root system, since the fungi are essential to nutrient absorption by the host and the fungi obtain their energy from the host much as if they were indeed root tissue. Thus the mycorrhizal fungi can be regarded as organs of producer plants. Mycophagists that feed on mycorrhizal fungi are then grazers. Grazing of mycorrhizal fungi accounts for about 75 percent of the small mammal mycophagy in terms of the reports listed later in this paper, evaluated as known or presumed mycorrhizal taxa (Trappe, 1962, 1971). If only reports of stomach contents are considered, the percentage is considerably higher. Mycophagy of saprophytes, necrotrophic symbionts, or predators, on the other hand, can be regarded as part of the decomposer process and accounts for about 25 percent of the reports. Many, perhaps most mycophagists feed on both categories of fungi and thereby participate in both processes.

Small mammal mycophagy seems surely to be a significant energy transfer process in ecosystems, but it remains to be quantitatively assessed. We are aware of only one paper with enough information to present a small mammal-fungus carbon budget for a short period: C. Smith (1965) estimated the caloric consumption of different food sources by the red squirrel *(Tamiasciurus hudsonicus)* for the month of August in western Washington. During this time, mycophagy accounted for about 73 percent of the squirrels' caloric intake, even though coniferous seeds and blueberries were also available (Fig. 1). Data from several other papers were not usable since percent volume and frequency values reported are useless without estimates of food consumption, weight, caloric value, stomach size, food density, etc. Modeling can not proceed until integrated studies on mycophagist food habits and fungal production are completed.

Despite inadequate information, mycophagy is clearly important to mammals and fungi alike. More extensive and definitive information is badly needed, particularly for understanding the dynamics of small mammal populations and for ecosystem modeling; nutrient flow is not a simple matter of diffusion through arbitrarily generalized functional groups such as primary producers, consumers, or decomposers.

Figure 1. *Tamiasciurus hudsonicus* caloric (kcal. 1000 gm^{-1}) consumption for August. (Smith, C., 1965) Percent of August consumption enclosed in parentheses.



The Reciprocal Lists

The literature reports of small mammal mycophagy are compiled in the following lists by taxa of both fungi and mammals. The lists are intended to provide a broad overview indexed to the original sources. Because any such listing is subject to limitations, restraint should be used in drawing detailed inferences from the lists themselves. Use them only as portals to the original literature. Keep in mind that the lists exclude lichens; that while coverage is almost complete for the North American literature, several references from other parts of the world could not be located; and that some taxa undoubtedly have been misidentified by some original authors.

No single system of taxonomy enjoys complete acceptance for either the fungi or the mammals. We have accordingly followed the classification and nomenclature of the more comprehensive compendia where possible, recognizing that many readers may prefer a somewhat different system. The fungal classification has been drawn from various sources, including Singer (1962) for Agaricales, Overholts (1953) for Polyporaceae, and Smith (1951) for Gasteromycetes. Mammal classification follows Hall and Kelson (1959), Jackson (1928), Johnson (1968), and Johnson and Ostenson (1959) for North American species and Ognev (1940, 1950) for Eurasian species.

The lists are alphabetical except for classes and orders. All known synonyms of a taxon have been cross-indexed to a single name; we do not intend any novel taxonomic decisions in this process, since the conclusions were drawn entirely from the literature, not from personal examination of types or other specimens.

Fungi listed with asterisk have been reported as demonstrated or probable mycorrhizal species in Trappe (1962, 1971), Gerdemann and Trappe (1974), or elsewhere.

Fungi and the Animals That Eat Them

CLASS PHYCOMYCETES
Unspecified taxa: *Potorous tridactylus apicalis* (Guiler, 1971).
ORDER OOMYCETALES
See Class Phycomycetes. Apparently this order has never been used.
ORDER MUCORALES
FAMILY ENDOGONACEAE
Endogone spp.: *Blarina brevicauda* (Hamilton, 1941b; Linzey and Linzey, 1973; Whitaker, 1962; Whitaker and Ferraro, 1963); *Clethrionomys gapperi gapperi* (Linzey and Linzey, 1973; Whitaker, 1962; Williams and Finney, 1964); Cricetidae (Dowding, 1959). *Eutamias* spp. Dowding, 1955, 1959; Whitaker, 1962); *Lagurus curtatus* (Whitaker, 1962); *Microtus chrotorrhinus* (Linzey and Linzey, 1973); *M. longicaudus* (Williams and Finney, 1964; *M. ochrogaster* (Zimmermann, 1965, 1966); *M. oeconomus macfarlandi* (Dowding, 1955; Whitaker, 1962); *M. pennsylvanicus* (Whitaker, 1962; Zimmermann, 1966); *M. pinetorum* (Linzey and Linzey, 1973; Whitaker, 1962); *Mus musculus* (Calhoun, 1941; Whitaker, 1962, 1966); *Napaeozapus insignis insignis* (Linzey and Linzey, 1973; Whitaker, 1962, 1963a); *Ochotona* spp. (Dowding, 1959); *O. princeps* (Whitaker, 1962; Zimmermann, 1965); *Onychomys leucogaster* (Whitaker, 1962); *Oryzomys palustris* (Negus, Gould, and Chipman, 1961); *Peromyscus gossypinus* (Calhoun, 1941; Whitaker, 1962); *P. leucopus* (Calhoun, 1941; Linzey and Linzey, 1973; Whitaker, 1962, 1963b, 1966); *P. leucopus noveboracensis* (Hamilton, 1941b); *P. maniculatus* (Dowding, 1955; Linzey and Linzey, 1973; Whitaker, 1962; Williams and Finney, 1964); *P. maniculatus bairdii* (Whitaker, 1966); *P. maniculatus gracilis* (Hamilton, 1941b); *Phenacomys intermedius* (Williams and Finney, 1964), Rodentia (Ingold, 1961, 1966; Kessler and Blank, 1972); *Sorex* spp. (Thaxter, 1922); *S. bendirii* (Whitaker and Maser, 1976); *S. cinereus* (Whitaker, 1962); *S. fumeus* (Linzey and Linzey, 1973; Whitaker, 1962); *S. trowbridgii* (Whitaker and Maser, 1976); *S. vagrans* (Whitaker and Maser, 1976); *S. vagrans pacificus* (Whitaker and Maser, 1976); *S. vagrans yaquinae* (Whitaker and Maser, 1976); *Soricidae* (Dowding, 1959); *Synaptomys cooperi cooperi* (Conner, 1960; Hamilton, 1941a, 1942; Hatt, 1930; Linzey and Linzey, 1973; Whitaker, 1962); *S. cooperi gossii* (Burt, 1928; Hamilton, 1941b); Talpidae (Dowding, 1959); *Zapus hudsonicus* (Whitaker, 1962); *Z. princeps* (Williams and Finney, 1964); *Z. trinotatus* (Whitaker, 1962).
**E. flammicorona* Trappe and Gerdemann: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
**E. lactiflua* Berk. and Broome: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974); *Zapus trinotatus* (Gerdemann and Trappe, 1974).
E. pisiformis Link *ex* Fries: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
E. macrospora: See *G. macrocarpa. (E. macrospora* was an erroneous citation for *E. macrocarpa).*
**Glomus caledonius* (Nicol. and Gerd.) Trappe and Gerdemann: *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
**G. fasciculatus* (Thaxt. *sensu* Gerdemann) Gerdemann and Trappe: *Clerthrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Lagurus curtatus* (Dowing, 1955); *Microtus pennsylvanicus* (Bakerspigel, 1956, 1958; Whitaker, 1962); *Ochotona princeps* (Dowding, 1955); *Onychomys leucogaster* (Dowding, 1955); *Peromyscus maniculatus* (Bakerspigel, 1956, 1958; Dowding, 1955; Whitaker, 1962); *Sciurus aberti* (Stephenson, 1975); *Zapus princeps* (Bakerspigel, 1956; Whitaker, 1962); *Z. trinotatus* (Gerdemann and Trappe, 1974).
**G. macrocarpus* Tul. and Tul.: *Blarina* spp. (Hamilton, 1941b); *B. brevicauda* (Diehl, 1939); *Clethrionomys* spp. (Hamilton, 1941b); *C. gapperi gapperi* (Diehl, 1939); *Peromyscus* spp. (Hamilton, 1941b); *P. leucopus novoboracensis* (Diehl, 1939); *P maniculatus* (Harling and McClaren, 1970); *Sorex cinereus* (Diehl, 1939; Hamilton, 1941b); *S. fumeus* (Diehl, 1939; Hamilton, 1941b); *Synaptomys cooperi cooperi* (Diehl, 1939); *S. cooperi gossii* (Hamilton, 1941b).
**G. macrocarpus* Tul. and Tul. *var.* **macrocarpus: Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
**G. microcarpus* Tul. and Tul.: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
**G. monosporus* Gerdemann and Trappe: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Zapus trinotatus* (Gerdemann and Trappe, 1974).
G. pulvinatus (Henn.) Trappe and Gerdemann: *Zapus princeps* (Dowding, 1955; Whitaker, 1962).
**Sclerocystis rubiformis* Gerdemann and Trappe: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974); *Zapus trinotatus* (Gerdemann and Trappe, 1974).

CLASS ASCOMYCETES
ORDER PLECTASCALES
FAMILY ELAPHOMYCETACEAE
Elaphomyces spp.: *Neotoma fuscipes annectens* (Parks, 1922); Rodentia (Ingold, 1961, 1966; Reess and Fisch, 1887); *Sciurus aberti* (Stephenson, 1975).
**E. granulatus* Fr.: Leporidae (Hawker, 1954); Rodentia (Hastings and Mottram, 1916; Hawker, 1954; Ingold, 1953); Sciuridae (Bulle-, 1922; Dowding, 1959); *Sciurus carolinensis carolinensis* (Ingold, 1973); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
ORDER DOTHIDEALES
FAMILY DOTHIDEACEAE
Dibotryon spp: *Sciurus carolinensis carolinensis* (Dudderar, 1967).
ORDER HYPOCREALES
FAMILY HYPOCREACEAE
Hypomyces spp.: *Tamiasciurus hudsonicus hudsonicus* (Seton, 1928).
ORDER PEZIZALES
FAMILY HELVELLACEAE
Helvella spp.: *Oryctolagus cuniculus* (Kumerloeve, 1956).
H. lacunosa Afz. *ex* Fr.: *Neotoma fuscipes* (Linsdale and Tevis, 1951).
H. mitra: See *H. lacunosa.*
Paxina acetabulum (L. *ex* St. Amans) Kuntze: *Neotoma fuscipes* (Linsdale and Tevis, 1951).
FAMILY MORCHELLACEAE
Tamiasciurus hudsonicus hudsonicus (Buller, 1922).
Morchella spp.: *Lepus europaeus* (Kumerloeve, 1956).
FAMILY PEZIZACEAE
**Geopora cooperi* Harkness: *Sciurus aberti aberti* (Stephenson, 1975).
Peziza spp.: *Neotoma fuscipes* (Linsdale and Tevis, 1951); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
P. emileia Cke: Neotoma fuscipes (Linsdale and Tevis, 1951).
ORDER TUBERALES
Peromyscus boylei (Jameson, 1952); *Spermophilus* spp. (Bessey, 1935); *Tamiasciurus douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
FAMILY TUBERACEAE
Leporidae (Kavaler, 1965); *Neotoma* spp. (Smith, 1938); Rodentia (Christenson, 1951; Kavaler, 1965; Lilly and Barnett, 1951; Mehrotra, 1967; Smith, 1938); Sciuridae (Kavaler, 1965).
Balsamia spp.: *Clethrionomys glareolus* (Drożdż, 1966).
**B. vulgaris* Vitt.: *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *S. vulgaris* (DuReau, 1912; Hatt, 1929).
**Fischerula subcaulis* Trappe: *Microtus oregoni* (Trappe, 1975).
Genea spp.: *Clethrionomys glareolus* (Drożdż, 1966).
Hydnotrya spp.: *Clethrionomys glareolus* (Drożdż, 1966).
Tuber spp.: *Clethrionomys glareolus* (Drożdż, 1966); Geomyidae (Parks, 1922); *Neotoma fuscipes* (Linsdale and Tevis, 1951); Rodentia (Ingold, 1961, 1966); *Sciurus aberti aberti* (Keith, 1965; Stephenson, 1975).
**T. aestivum* Vitt.: Rodentia (Hawker, 1954).
T. candidum Harkn: see *T. rufum* var. *nitidum.*
**Tuber rufum* var. **nitdium* (Vitt.) Fischer: *Neotoma* spp. (Parks, 1921); Rodentia (Parks, 1921).
CLASS BASIDIOMYCETES
ORDER UREDINALES
Peromyscus leucopus (Calhoun, 1941).
FAMILY PUCCINIACEAE
Peridermium harknessii Moore: *Tamiasciurus hudsonicus hudsonicus* (Smith, C. 1965).
FAMILY MELAMPSORACEAE
Cronartium ribicola A. Fisch.: *Sciuridae* (Spaulding, 1922); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
ORDER TREMALES
FAMILY DACRYMYCETACEAE
Calocera viscosa (Fr.) Fr.: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932).
ORDER AGARICALES
Sciurus vulgaris leucourus (Barrett-Hamilton and Hinton, 1921).
FAMILY AGARICACEAE
Neotoma cinerea orolestes (Finley, 1958); *N. floridana magister* (Newcombe, 1930); *N. fuscipes annectens* (Parks, 1922); *Sciurus carolinensis carolinensis* (Styan, 1946); *S. niger niger* (Baumgartner, 1939a, 1939b).
Agaricus spp.: *Neotoma floridana magister* (Newcombe, 1930); *Sciurus aberti aberti* (Keith, 1965).
A. campestris L. *ex* Fr.: *Potorous tridactylus apicalis* (Guiler, 1971); *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
Coprinus spp.: *Blarina brevicauda* (Hamilton, 1930); *Didelphis virginiana* (Hamilton, 1958).
Lepiota spp.: *Sciurus aberti aberti* (Keith, 1965).
L. naucinoides: See *Leucoagaricus naucinus.*

Leucoagaricus naucinus (Fr.) Sing.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927).
Mycena epipterygia (Scott. *ex* Fr.) S. F. Gray: *Leporidae* (Hastings and Mottram, 1916).
Psalliota campestris: See *Agaricus campestris.*
FAMILY AMANITACEAE
Amanita spp.: Mammalia (Miller and Halls, 1969); Sciuridae (Miller and Halls, 1969); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hamilton, 1939, Smith, 1968); *T. hudsonicus minnesota* (Hamilton, 1943).
**A. muscaria* (L. *ex* Fr.) Pers. *ex* Hooker: Rodentia (Hastings and Mottram, 1916); Sciuridae (Hastings and Mottram, 1916); *Sciurus aberti aberti* (Keith, 1965); *S. carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927; Krieger, 1967; Metcalf, 1925; Rue, 1967).
**A. phalloides* (Vaill. *ex* Fr.) Secr.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
**A. rubescens* (Pers. *ex* Fr.) S. F. Gray: Leporidae (Hastings and Mottram, 1916).
**A. vaginata* (Bull. *ex* Fr.) Vitt.: *Sciurus aberti aberti* (Keith, 1965); *Tamias striatus lysteri* (Allen, 1938, Fraleigh, 1929); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Aminitopsis vaginata varialba: See *Amanita vaginata.*
Pluteus atricapillus (Sect.) Sing.: *Neotoma fuscipes* (Linsdale and Tevis, 1951); *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
P. cervinus: See *P. atricapillus.*
P. nanus (Pers. *ex* Fr.) Kumm.: *Sciurus vulgaris exalbidus* (Ognev, 1940).
FAMILY BOLETACEAE
Neotoma fuscipes annectens (Parks, 1922); Rodentia (Miller and Halls, 1969); Sciuridae (Miller and Halls, 1969).
Boletinus cavipes: See *Suillus cavipes.*
**B. pictus* (Peck) Peck: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).
Boletus spp.: *Eutamias quadrimaculatus* (Tevis, 1952); *Lemmus lemmus* (Ognev, 1948); *Neotoma floridana magister* (Newcombe, 1930; Poole, 1940); Sciuridae (Odell, 1926); *Sciurus aberti aberti* (Keith, 1965); *S. carolinensis carolinensis* (Cross, 1942; Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922; Klugh, 1927; Krieger, 1967; Seton, 1929; Smith, 1968).
B. badius: See *Xerocomus badius.*
B. bovinus: See *Suillus bovinus.*
**B. calopus* Fr.: Sciuridae (Cooke, 1890); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916).
B. castaneus: See *Gyroporus castaneus.*
B. chrysenteron: See *Xerocomus chrysenteron.*
**B. edulis* Bull. *ex* Fr.: Rodentia (Hastings and Mottram, 1916); *Sciurus vulgaris* (Ognev, 1940).
B. flavidus: See *Suillus flavidus.*
**B. impolitus* Fr.: Sciuridae (Cooke, 1890); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916).
B. luteus: See *Suillus luteus.*
**B. mirabilis* Murr.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
B. pachypus: See *B. calopus.*
B. pallidus Frost: *Neotoma floridana magister* (Poole, 1940).
B. piperatus: See *Suillus piperatus.*
B. rufus: See *Leccinum aurantiacum.*
B. scaber: See *Leccinum scabrum.*
B. subtomentosus: See *Xerocomus subtomentosus.*
B. variegatus: See *Suillus variegatus.*
B. versipellis Fr.: See *Leccinum versipellis.*
**Gyroporus castaneus* (Bull. *ex* Fr.) Quél.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
**Leccinum aurantiacum* (Bull.) S. F. Gray: *Sciurus vulgaris* (Ognev, 1940); *S. vulgaris exalbidus* (Ognev, 1940; Stakhrovskii, 1932).
**L. scabrum* (Fr.) S. F. Gray: Sciuridae (Massee, 1913); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *S. vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *S. vulgaris exalbidus* (Ognev, 1940); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hatt, 1929).
**L. versipellis* (Fr.) Snell: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
**Suillus bovinus* (L. *ex* Fr.) Kuntze: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *S. vulgaris exalbidus* (Ognev, 1940); *Tamiasciurus husonicus hudsonicus* (Hatt, 1929).
**S. cavipes* (Opat.) A. H. Sm. and Thiers: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
**S. flavidus* (Fr.) Sing.: Rodentia (Hastings and Mottram, 1916).
**S. granulatus* (Fr.) Kuntze: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
**S. lakei* (Murr.) A. H. Sm. and Thiers: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
**S. luteus* (L. *ex* Fr.) S. F. Gray: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *S. vulgaris exalbidus* (Ognev 1940); *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

S. piperatus (Bull. *ex* Fr.) Kuntze: *Sciurus vulgaris exalbidus* (Ognev, 1940).
S. subolivaceus A. H. Sm. and Thiers: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
S. tomentosus (Kauffm.) Sing., Snell, and Dick: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
S. variegatus (Sw. *ex* Fr.) Kuntze: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensus* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Xerocomus badius (Fr.) Kühner *ex* Gilbert: Leporidae (Buller, 1922); Rodentia (Hastings and Mottram, 1916).
X. chrysenteron (Bull. *ex* St. Amans) Quél.: Rodentia (Hastings and Mottram, 1916); *Sciurus vulgaris exalbidus* (Ognev, 1940).
X. subtomentosus (L. *ex* Fr.) Quél.: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *S. vulgaris exalbidus* (Ognev, 1940).

FAMILY COPRINACEAE

Hypholoma spp.: See *Psathyrella* spp.
H. fasiculare: See *Naematoloma fasiculare* in Strophariaceae.
Psathyrella spp.: *Sciurus aberti aberti* (Keith, 1965); *Tamiasciurus hudsonicus hudsonicus* (Seton, 1929).

FAMILY CORTINARIACEAE

Cortinarius spp.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hardy, 1949; Hatt, 1929; Seton, 1929; Smith, C., 1965).
C. collinitus (Pers. *ex* Fr.) Fr.: Rodentia (Hastings and Mottram, 1916).
C. distans Peck: Rodentia (Miller and Halls, 1969).
C. varius (Schaeff. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
Flammula sapinea: See *Gymnopilus sapineus.*
Gymnopilus sapineus (Fr.) Maire: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Inocybe spp.: *Neotoma floridana magister* (Newcombe, 1930; Poole, 1940); *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).
Rozites caperata (Pers. *ex* Fr.) Karst.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

FAMILY CREPIDOTACEAE

Crepidotus malachius: See *C. nephrodes.*
C. nephrodes (Berk. and Curt.) Sacc.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).

FAMILY GOMPHIDACEAE

Chroogomphus rutilus: See *Gomphidius rutilus.*
C. tomentosus: See *Gomphidius tomentosus.*
Gomphidius glutinosus (Shaeff. *ex* Fr.) Fr.: *Sciurus vulgaris exalbidus* (Ognev, 1940).
G. rutilus (Schaeff. *ex* Fr.) Lund. and Nannf.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
G. subroseus Kauffm.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
G. tomentosus Murr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

FAMILY HYGROPHORACEAE

Hygrocybe miniata (Scop. *ex* Fr.) Kumm.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
Hygrophorus chrysodon (Batsch *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
H. hypothejus (Fr.) Fr.: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
H. miniatus: See *Hygrocybe miniata.*
H. pudorinus (Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Odell, 1925).

FAMILY PAXILLACEAE

Hygrophoropsis aurantiaca (Wulf *ex* Fr.) Maire: Leporidae (Hastings and Mottram, 1916); Rodentia (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Paxillus atrotomentosus (Batsch *ex* Fr.) Fr.: Rodentia (Hastings and Mottram, 1916).
P. involutus (Batsch *ex* Fr.) Fr.: Leporidae (Hastings and Mottram, 1916); Rodentia (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

FAMILY RUSSULACEAE

Clethrionomys rutilus mikado (Murata, 1976).
Lactarius spp.; Rodentia (Miller and Halls, 1969); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
L. deliciosus (L. *ex* Fr.) S. F. Gray: *Sciurus carolinensis carolinensis* (Barkalow and Shorten, 1973); *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
L. lignyotus (Fr. *ex* Fr.) Fr.: *Clethrionomys gapperi gapperi* (Hamilton, 1941b).
L. necator (Bull. *em.* Pers. *ex* Fr.) Karst.: Rodentia (Hastings and Mottram, 1916).
L. piperatus (L. *ex* Fr.) S. F. Gray: Rodentia (Miller and Halls, 1969); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hardy, 1949; Hatt, 1929).
L. rufus (Scop. *ex* Fr.) Fr.: Rodentia (Hastings and Mottram, 1916).
L. torminosus (Schaeff. *ex* Fr. S. F. Gray: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932).
L. turpis: See *Lactarius necator.*
L. uvidus (Fr. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
Russula spp.: *Clethrionomys glareolus* (Drożdż 1966); *Lemmus lemmus* (Ognev, 1948); *Napa-*

eozapus insignis insignis (Sheldon, 1934); *Neotoma floridana magister* (Newcombe, 1930; Poole, 1940); Sciuridae (Dowding, 1955); *Sciurus aberti aberti* (Keith, 1965); *S. carolinensis carolinensis* (Cross, 1942; Dudderar, 1967; Murrill, 1910); *Tamias striatus lysteri* (Allen, 1938; Fraleigh, 1929; Sheldon, 1936); *Tamiasciurus hudsonicus fremonti* (Hatt, 1943); *T. hudsonicus hudsonicus* (Buller, 1920, 1922; Klugh, 1927).

**R. adusta* (Pers. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

**R. alutacea* (Pers. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

**R. bicolor* Burl.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. bicolor var. *constans:* See *Russula bicolor.*

R. bicolor var. *reticulispora:* See *Russula bicolor.*

**R. blackfordae* Peck: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. brevipes* Peck: *Tamiasciurus douglasi douglasi* (Smith, C., 1965).

**R. consobrina* (Fr. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. decorans* Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. delica: see *R. brevipes.*

R. depallens: See *Russula pulchella.*

R. disparilis Burl.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. emetica* (Schaeff. *ex* Fr.) Pers. *ex* Fr.: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* Hatt, 1929).

**R. emetica* ssp. **fragilis* (Pers. *ex* Fr.) Sing.: *Tamiasciurus hudsonicus* (Smith, C., 1965).

R. fragilis: See *Russula emetica* ssp. *fragilis.*

R. mariae Peck: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

**R. nigricans* (Bull. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. ochroleuca* (Pers. *ex* Fr.: *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916).

R. pallidostraminea nom. prov.: Tamiasciurus hudsonicus hudsonicus (Smith, C., 1965).

**R. pulchella* Borsc.: *Tamiaciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. rosea* Quél.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. rosipes (Secr.) Bres.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

**R. rubra* (Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

**R. xerampelina* (Schaeff. *ex* Secr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. xerampelina var. isabelliniceps: See *R. xerampelina.*

FAMILY STROPHARIACEAE

Kuehneromyces mutabilis (Schaeff. *ex* Fr.) Sing. and A. H. Sm.: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932).

Naematoloma fasiculare (Huds *ex* Fr.) Karst.: *Sciurus vulgaris* (Moffat, 1923); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hatt, 1929).

Pholiota spp.: *Sciurus vulgaris* (Ognev, 1940).

P. carbonaria (Fr.) Sing.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

P. discolor (Pk.) Sacc.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968).

P. lenta (Pers. *ex* Fr.) Sing.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965).

P. mutabilis: See *Kuehneromyces mutabilis.*

FAMILY TRICHOLOMATACEAE

Armillaria spp.: *Sciurus vulgaris* (Ognev, 1940).

A. mellea (Vahl in Fl. Dan. *ex* Fr.) Karst.: Sciuridae (Miller and Halls, 1969); *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hatt, 1929).

Clitocybe spp.: *Eutamias quadrimaculatus* (Tevis, 1952); *Sciurus vulgaris* (Ognev, 1940); *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

C. brumalis (Fr.) Quél.: Leporidae (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

C. maxima (Fl. Wett. *ex* Fr.) Kumm.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

C. monodelpha Morg.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

**C. odora* (Bull. *ex* Fr.) Kumm.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

C. virens: See *C. odora.*

Collybia dryophila (Bull. *ex* Fr.) Kumm.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

C. maculata (A. and S. *ex* Fr.) Quél.: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

C. radicata: See *Oudemansiella radicata.*

C. velutipes: See *Flammulina velutipes.*

Flammulina velutipes (Curt. *ex* Fr.) Sing.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain 1968).

Lentinus lepideus (Fr. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

**Lepista personata* (Fr. *ex* Fr.) Cke.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

Lyophyllum ulmarium (Bull. *ex* Fr.) Kühner: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

Marasmius spp.: *Orcytolagus cuniculus* (Kumerloeve, 1956).

Oudemansiella radicata (Relh. *ex* Fr.) Sing.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927).

Tricholoma spp.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

T. equestre: See *T. flavovirens.*

T. flavovirens (Pers. *ex* Fr.) Lund.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Odel, 1925).
T. personatum: See *Lepista personata.*
T. terreum (Schaeff. *ex* Fr.) Kumm.: *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916).
ORDER APHYLLOPHORALES
FAMILY CANTHARELLACEAE
Cantharellus aurantiacus: See *Hygrophoropsis aurantiaca* in Paxillaceae.
C. cibarius Fr.: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922; Hatt, 1929; Klugh, 1927).
C. floccosus: See *Gomphus floccosus.*
Gomphus floccosus (Schw.) Sing.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
FAMILY CLAVARIACEAE
Clavaria spp.: *Neotoma floridana magister* (Newcombe, 1930; Poole, 1930); *Tamiasciurus hudsonicus hudsonicus* (Smith, 1968).
C. aurea: See *Ramaria aurea.*
C. flava: See *Ramaria flava.*
C. pyxidata: See *Clavicorona pyxidata.*
Clavicorona pyxidata (Fr.) Poty: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
Ramaria aurea (Fr.) Quél.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927).
R. flava (Fr.) Quél.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Sparassis crispa Fr.: Leporidae (Hastings and Mottram, 1916).
FAMILY HYDNACEAE
Hericium caput-ursi (Fr.) Banker: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
Hydnum spp.: *Tamiasciurus hudsonicus hudsonicus* (Smith, 1968).
H. caput-ursi: See *Hericium caput-ursi.*
H. erinaceus Bull.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
H. fuligineo-violaceum Kalchb. in Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
H. imbricatum L. *ex* Fr. *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
H. repandum L. *ex* Fr.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
FAMILY POLYPORACEAE
Sciurus griseus griseus (Grinnel and Storer, 1924).
Daedalea spp.: *Sciurus carolinensis carolinensis* (Dudderar, 1967).
Fomes fomentarius (L. *ex* Fr.) Kickx: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
F. pinicola (Swartz *ex* Fr.) Cooke: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).
Pleurotus spp.: *Sciurus niger niger* (Packard, 1956).
P. ostreatus (Jacq. *ex* Fr.) Kumm.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927).
P. ulmarius: See *Lyophyllum ulmarium.*
Polyporus spp.: *Neotoma cinerea orolestes* (Warren, 1920); *Sciurus carolinensis carolinensis* (Dudderar, 1967; *Spermophilus lateralis* (Gordon, 1943); *Sylvilagus palustris paludicola* (Blair, 1936); *Tamiasciurus hudsonicus fremonti* (Hatt, 1943); *T. hudsonicus hudsonicus* (Hardy, 1949; Smith, 1968); *T. hudsonicus loquax* (Layne, 1954).
P. amarus Hedgc.: Sciuridae (Boyce, 1920); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
P. betulinus Bull. *ex* Fr.: Leporidae (Hastings and Mottram, 1916); *Sciurus vulgaris* (Ognev 1940); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
P. picipes Fr.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
P. sulphureus Bull. *ex* Fr.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
P. varius Fr.: *Neotoma fuscipes* (Linsdale and Tevis, 1951).
Polysticus spp.: See *Polyporus* spp.
FAMILY STEREACEAE
Stereum hirsutum Willdenon *ex* Fr.: *Sciurus carolinensis carolinensis* (Murrill, 1910).
ORDER HYMENOGASTRALES
FAMILY HYMENOGASTRACEAE
Rodentia (Gäumann and Dodge, 1928).
Alpova diplophloeus (Zeller and Dodge) Trappe: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
Gautieria spp.: *Neotoma* spp. (Parks, 1919); *N. fuscipes annectens* (Parks, 1922); *Sciurus aberti aberti* (Stephenson, 1975); *S. griseus griseus* (Stienecker and Browning, 1970).
G. graveolens Vitt.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, 1965; Smith, C., 1965).
G. morchelliformis Vitt.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Hydnangium spp.: *Neotoma fuscipes annectens* (Parks, 1922).
Hymenogaster spp.: *Blarina brevicauda* (Whitaker, 1962; Whitaker and Ferraro, 1963); *Clethrionomys gapperi gapperi* (Whitaker, 1962); *C. glareolus* (Drożdż, 1966); *Microtus oeconomus macfarlandi* (Whitaker, 1962); *Napaeozapus insignis insignis* (Whitaker, 1962, 1963a);

Neotoma fuscipes annectens (Parks, 1922); Rodentia (Ingold, 1961, 1966); *Zapus hudsonius* (Whitaker, 1962).

**H. tener* Berk.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

Martellia spp.: *Sciurus aberti aberti* (Stephenson, 1975).

Rhizopogon spp.: *Clethrionomys glareolus* (Drożdż, 1966); Rodentia (Ingold, 1966; Miller and Halls, 1969); Sciuridae (Miller and Halls, 1969); *Sciurus aberti aberti* (Stephenson, 1975); *S. griseus griseus* (Stienecker and Browning, 1970).

R. diplophloeus: See *Alpova diplophloeus.*

**R. luteolus* Fr. and Nordh.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. maculatus* Zeller and Dodge: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. occidentalis* Zeller and Dodge: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. pachyphloeus: See *Alpova diplophloeus.*

R. provincialis: See *R. vulgaris.*

**R. roseolus* Corda *sensu* A. H. Sm.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. rubescens* (Tul.) Tul.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).

**R. vinicolor* Sm.: *Tamiasciurus douglasi douglasi* (Fogel, 1976).

**R. viridis* Zeller and Dodge: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. vulgaris* (Vitt.) M. Lange: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**Truncocolumella citrina* Zeller: *Tamiasciurus douglasi douglasi* (Fogel, 1976); *T. hudsonicus hudsonicus* (Smith, C., 1965).

ORDER HYSTERANGIALES

FAMILY HYSTERANGIACEAE

Rodentia (Gäumann and Dodge, 1928).

Hysterangium spp.: *Neotoma* spp.: (Parks, 1919); *N. fuscipes annectens* (Parks, 1922); *Sciurus aberti aberti:* (Stephenson, 1975); *S. griseus griseus* (Stienecker and Browning, 1970).

FAMILY MELANOGASTRACEAE

Melanogaster spp.: *Clethrionomys glareolus* (Drożdż, 1966); *Neotoma* spp. (Parks, 1919); *N. fuscipes* (Linsdale and Tevis, 1951); *N. fuscipes annectens* (Parks, 1922); *Sciurus griseus griseus* (Stienecker and Browning, 1970).

**M. ambiguus* (Vitt.) Tul.: Sciuridae (Langham, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

M. broomeianus Berk. *in* Tul.: Leporidae (Hawker, 1954).

M. variegatus (Vitt.) Tul. *emend.* Zeller and Dodge: *Microtus pennsylvanicus* (Bakerspigel, 1958); *Peromyscus maniculatus* (Bakerspigel, 1958).

M. variegatus var. *broomeianus:* See *M. broomeianus.*

ORDER LYCOPERDALES

Dasypus novemcinctus mexicanus (Kalmbach, 1944); Phascolomidae (Troughton, 1947).

FAMILY GEASTERACEAE

Geastrum spp.: *Tamias striatus griseus* (Schmidt, 1931).

FAMILY LYCOPERDACEAE

Neotoma albigula warreni (Finley, 1958); *Tamias striatus fisheri* (Tunis, 1971).

Castoreum spp.: Leporidae (Cleland, 1935); Marsupialia (Cleland, 1935).

C. radicatum Cke. and Mass.: Marsupialia (Cunningham, 1942).

Lycoperdon spp.: *Apodemus sylvaticus* (Miller, 1954); *Neotoma cinerea* (Dalquest, 1948); *N. cinerea occidentalis* (Taylor, 1920); *N. floridana magister* (Poole, 1940); *Oryctolagus cuniculus* (Kumerloeve, 1956); *Sciurus aberti aberti* (Keith, 1965); *S. carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus loquax* (Connor, 1960).

**L. gemmatum* Batsch: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).

L. pyriforme Pers.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

Mesophellia spp.: Leporidae (Cleland, 1936; Cunningham, 1942); Marsupialia (Cleland, 1935; Cunningham, 1942).

M. arenaria Berk.: Leporidae (Cunningham, 1942); Macropodidae (Cunningham, 1942); Marsupialia (Cunningham, 1942); Permelidae (Cunningham, 1942).

M. pachythrix (Cke. and Mass.) Lloyd: Leporidae (Cleland, 1935).

ORDER SCLERODERMATALES

FAMILY SCLERODERMATACEAE

Scleroderma spp.: *Oryctolgus cuniculus* (Kumerloeve, 1956).

**S. citrinum* Pers.: *Neotoma floridana magister* (Newcombe, 1930).

S. hypogaeum Zeller: *Neotoma fuscipes* (Linsdale and Tevis, 1951).

S. vulgara: See *S. citrinum.*

MISCELLANEOUS REPORTS

Unnamed fungi: *Apodemus flavicollis* (Drożdż, 1966; Zemanek, 1972); *A. sylvaticus* (Hansson, 1970; 1971; Holišová, 1960; Southern, 1964); *Clethrionomys* spp. (Palmer, 1954; Walker, 1964); *C. gapperi athabascae* (Harper, 1956); *C. gapperi gapperi* (Connor, 1960; Doutt, Heppenstall, and Guilday, 1967; Jackson, 1961; Larrison, 1970; Linzey and Linzey, 1973); *C. gapperi paludicola* (Doutt, Heppenstall, and Guilday, 1967); *C. gapperi rhoadsii* (Connor, 1953); *C. gapperi rupicola* (Doutt, Heppenstall, and Guilday, 1967); *C. glareolus* (Hansson, 1969, 1971; Holišová, 1971, 1972; Miller, 1954; Ognev, 1950; Southern, 1964; Zem-

anek, 1972); *C. rufocanus* (Hansson, 1969); *Dasypus novemcinctus mexicanus* (Fitch, Goodrum, and Newman, 1952; Kalmbach, 1944; Miller and Halls, 1969); *Dicrostonyx groenlandicus* (Dunaeva and Kucheruk, 1941; Watson, 1956); *D. torquatus* (Ognev, 1948); *Didelphis virginiana* (Palmer, 1964; Sumner and Dixon, 1953); *Dipodomys* spp. (Cahalane, 1947; Palmer, 1954); *Eutamias* spp. (Cahalane, 1947; Gordon, 1943; Hamilton, 1939; Olin, 1961; Orr, 1949; Palmer, 1954; Walker, 1964); *E. cinereicollis cinereicollis* (Bailey, 1931); *E. minimus neglectus* (Hamilton, 1943); *E. minimus pictus* (Bailey, 1936); *E. quadrivittatus quadrivittatus* (Baliey, 1931; MacClintock, 1970); *E. speciosus* (Ingles, 1947; Tevis, 1953); *E. townsendii* (Larrison, 1970); *E. townsendii senex* (Bailey, 1936); *Glaucomys* spp. (Palmer, 1954); *G. sabrinus* (Cahalane, 1947; MacClintock, 1970; McKeever, 1960); *G. sabrinus fuscus* (Hamilton, 1943); *G. sabrinus macrotis* (Connor, 1960; Jackson, 1961); *G. volans* (Cahalane, 1947; Corbet, 1966; MacClintock, 1970; Ognev, 1940; Schwartz and Schwartz, 1959); *G. volans volans* (Connor, 1960); *Isoden obesulus* (Brazenor, 1950); *Lemmus lemmus* (Corbet, 1966; Marsden, 1964; Ognev, 1948); Leporidae (Rolfe and Rolfe, 1925); *Lepus europaeus* (Hansson, 1970); Macropodidae (Cleland, 1934); *Mastocomys* spp. (Walker, 1964); *Microdipodops* spp. (Cahalane, 1947); *Microtus agrestis* (Hansson, 1970, 1971); *M. pennsylvanicus* (Golley, 1960); *Neotoma* spp. (Hamilton, 1939); *N. cinerea* (Dalquest, 1948); *N. cinerea occidentalis* (Taylor, 1920); *N. cinerea orolestes* (Warren, 1942); *N. floridana* (Hall, 1955; Schwartz and Schwartz, 1959); *N. floridana attwateri* (Bailey, 1905; Rainey, 1956); *N. floridana magister* (Hamilton, 1943; Newcombe, 1930; Paradiso, 1969; Roberts and Early, 1952); *N. fuscipes* (Linsdale and Tevis, 1951); *N. fuscipes macrotis* Howel, 1926); *N. lepida lepida* (Barnes, 1922, 1927); *Papio cyncephalus* (Altman and Altman, 1970); *Perognathus parvus* (Johnson, 1961); *Peromyscus boylei* (Jameson, 1952); *P. leucopus* (Miller and Halls, 1969); *P. leucopus noveboracensis* (Hamilton, 1941b); *P. maniculatus* (Dalquest, 1948; Jameson, 1952; Miller and Halls, 1969; Schwartz and Schwartz, 1959; Walton, 1898); *P. maniculatus artemisiae* (Williams, 1959); *P. maniculatus bairdii* (Whitaker, 1966); *P. maniculatus gracilis* (Connor, 1960; Hamilton, 1941b); *P. maniculatus osgoodi* (Williams, 1959); *P. truei* (Bradford, 1974); Phascolomidae (Carter, Hill, and Tate, 1945); Peramelidae (Cleland, 1934); *Phenacomys intermedius mackenzii* (Harper, 1956); *Pitymys subterraneus* (Holišová, 1965); *P. tatricus* (Holišová, 1965); *Potorous tridactylus* (Brazenor, 1950); *P. tridactylus apicalis* (Guiler, 1971); Rodentia (Miller and Halls, 1969; Rolfe and Rolfe, 1925); Sciuridae (Brehm, 1895; Hamilton, 1939; Miller and Halls, 1969; Rolfe and Rolft, 1925); *Sciurus* spp. (Walker, 1964); *S. aberti aberti* (Bailey, 1931; Cahalane, 1947; MacClintock, 1970; Palmer, 1954; Patton, 1975; Seton, 1929; Stephenson, 1974); *S. carolinensis carolinensis* (Bailey, 1946; Ballou, 1927; Barber, 1954; Bernard, 1937; Burt, 1957; Cahalane, 1947; Cranbrook and Payn, 1962; Cross, 1942, 1946; Goodrum, 1940; Halls and Stransky, 1971; Hoffmeister and Mohr, 1957; Lyon, 1936; MacClintock, 1970; Martin *et al.*, 1951; Miller and Halls, 1969; Moore, 1943; Nelson, 1918; Palmer, 1954; Peterson, 1966; Robinson and Cowan, 1954; Schwartz and Schwartz, 1959; Shorten, 1962; Shorten and Courtier, 1955; Southern, 1964); *S. carolinensis hypophaeus* (Jackson, 1961; Larrison, 1970); *S. carolinensis pennsylvanicus* (Doutt, Heppenstall, and Guilday, 1967); *S. griseus griseus* (Cahalane, 1947; Miller and Halls, 1969; Sumner and Dixon, 1953); *S. kaibabensis* (Cahalane, 1947; Goldman, 1928; Hall, 1967; MacClintock, 1970; Nelson, 1918; Palmer, 1954); *S. niger cinerus* (Bailey, 1946); *S. niger niger* (Anthony and McSpadden, 1917; Allen, 1943; Barber, 1954; Baumgartner, 1939a, 1939b; Burt, 1957; Cahalane, 1947; Golley, 1962; Hall, 1955; Hoffmeister and Mohr, 1957; MacClintock, 1970; Matrin *et al.*, 1951; Moore, 1943; Palmer, 1954; Shafeldt, 1920); *S. niger rufiventer* (Larrison, 1970; Over and Churchill, 1941); *S. vulgaris* (Bourliere, 1956; Cranbrook and Payn, 1962; Lampio, 1967; Southern, 1964; Van Gelder, 1969); *S. vulgaris leucourus* (Shorten, 1959; 1962); *S. vulgaris orientis* (Abe, 1967); Soricidae (Martin *et al.*, 1951); *Spermophilus* spp. (Bourliere, 1956; Walker, 1964); *S. beecheyi* (Fitch, 1948; Linsdale, 1946); *S. lateralis chrysodeirus* (Bailey, 1936; Howell, 1938; Sumner and Dixon, 1953); *S. lateralis lateralis* (Bailey, 1931; Cahalane, 1947; Dalquest, 1948; Gordon, 1943; MacClintock, 1970; Seton, 1929); *S. richardsonii* (Hansen and Ueckert, 1970); *S. undulatus kennicottii* (Bee and Hall, 1956); *S. undulatus parryii* (Howell, 1938; Seton, 1971); *Spilogale* spp. (Howell, 1906); *S. putorius* (Bailey, 1946; Martin *et al.*, 1951); *Synaptomys cooperi cooperi* (Doutt, Heppenstall, and Guilday, 1967; Jackson, 1961; Martin *et al.*, 1951; Schwartz and Schwartz, 1959); *S. cooperi stonei* (Doutt, Heppenstall, and Guilday, 1967); Talpidae (Martin *et al.*, 1951; *Tamias* spp. Dalquest, 1948; Hamilton, 1939; Martin *et al.*, 1951); *T. striatus fisheri* (Bailey, 1946; Tunis, 1971); *T. striatus griseus* (Jackson, 1961); *T. striatus lysteri* (Allen, 1938; Doutt, Heppenstall, and Guilday, 1967; Gifford and Whitebread, 1951; Mearns, 1899; Seton, 1929); *T. striatus striatus* (Bailey, 1946; Cahalane, 1947; Golley, 1962; MacClintock, 1970; Schwartz and Schwartz, (1959); *Tamiasciurus* spp. (Bourliere, 1956; Palmer, 1954); *T. douglasi alholimbatus* (Bailey, 1936; Stevens, 1906); *T. douglasi douglasi* (Bailey, 1936; Broadbrooks, 1958; Cahalane, 1947; Dalquest, 1948; MacClintock, 1970; Nelson, 1918; Orr, 1949; Seton, 1929); *T. douglasi mollipilosus* (Bailey, 1936); *T. hudsonicus abieticola* (Golley, 1926); *T. hudsonicus dakotensis* (Over and Churchill, 1941); *T. hudsonicus fremonti* (Cahalane, 1947; Hatt, 1943; Olin, 1961); *T. hudsonicus hudsonicus* (Anthony and McSpadden, 1917; Burt, 1957; Cahalane, 1947; Cameron, 1956; Cram, 1924; Dalquest, 1948; Dice, 1921;

Hamilton, 1939; Jackson, 1931-1932; MacClintock, 1970; Marie, 1927; Martin *et al.*, 1951; Merriam, 1884; Murrill, 1902; Nelson, 1918; Peterson, 1966; Rand, 1948; Seagears, 1949, 1950; Seton, 1929; Van Gelder, 1969; Walton, 1903; Zim and Hoffmeister, 1955); *T. hudsonicus loquax* (Bailey, 1946; Connor, 1960; Doutt, Heppenstall, and Guilday, 1967; Grim and Roberts, 1950; Layne, 1954; Lyon, 1936; Paradiso, 1969; Roberts and Early, 1952); *T. hudsonicus lychnuchus* (Bailey, 1931); *T. hudsonicus minnesota* (Hamilton, 1943; Jackson, 1961; Over and Churchill, 1941); *T. hudsonicus mogollonensis* (Bailey, 1931); *T. hudsonicus preblei* (Harper, 1956); *T. hudsonicus richardsoni* (Bailey, 1936); *T. hudsonicus streatori* (Rust, 1946); *T. hudsonicus ventorum* (Barnes, 1922, 1927); *Vombatus hirsutus* (Brazenor, 1950).

Hypogoeus fungi, "truffles," hypogeous Gasteromycetes, basidiomycetous tubers, hypogeous Basidiomycetes, etc.

Apodemus sylvaticus (Watts, 1968); *Clethrionomys glareolus* (Watts, 1968); *Eutamias* spp. (Dowding, 1959); *E. amoenus* (Broadbrooks, 1958; Tevis, 1952); *E. quadrimaculatus* (Tevis, 1952, 1953); *E. townsendii* (Tevis, 1952, 1953); *Glaucomys sabrinus* (McKeever, 1960; Tevis, 1953); *Lepus europaeus* (Southern, 1964); Macropodidae (LeSouef and Burrell, 1926; Troughton, 1947); *Neotoma* spp. (Zeller, 1939); *N. cinerea* (Tevis, 1953); *Peromyscus boylei* (Tevis, 1953); *Phascolomys* spp. (LeSouef and Burrell, 1926); *Potorous* spp. (Troughton, 1943, 1944); Rodentia (Burnett, 1968; Gwynne-Vaughan, 1937); Sciuridae (Lohwag, 1932); *Sciurus griseus griseus* (Grinnel and Storer, 1924; Tevis, 1953); *Spermophilus* spp. (Dowding, 1959); *S. beecheyi* (Tevis, 1953); *Tamiasciurus douglasi douglasi* (Zeller, 1939).

Animals and the Fungi They Eat

CLASS MAMMALIA
ORDER MARSUPIALIA
Mesophellia spp.; *M. arenaria; Castoreum* spp.; *C. radicatum.*
FAMILY DIDELPHIDAE
Didelphis virginiana Kerr—opossum: *Coprinus* spp.; fungi.
FAMILY PERAMELIDAE
Mesophellia arenaria; fungi.
Isoden obesulus (Shaw)—short-nosed bandicoot: fungi.
FAMILY PHASCOLOMIDAE
Lycoperdales; fungi.
Phascolomys spp.: hypogeous fungi.
Vombatus hirsutus (Perry)—common wombat: fungi.
FAMILY MACROPODIDAE
Mesophellia arenaria; hypogeous fungi; fungi.
Potorous spp.: hypogeous fungi.
P. tridactylus Kerr—dark rat-kangaroo: fungi.
P. tridactylus apicalis (Gould): *Agaricus campestris; Oomycetales;* fungi.
ORDER INSECTIVORA
FAMILY SORICIDAE
Endogone spp.
Blarina spp.: *Glomus macrocarpus.*
B. brevicauda (Say)—short-tailed shrew: *Coprinus* spp.; *Endogone* spp.; *Glomus macrocarpus; Hymenogaster* spp.
Sorex spp.: fungi.
S. bendirii (Merriam)—Pacific water shrew: fungi.
S. cinereus Kerr—masked shrew: *Endogone* spp.; *Glomus macrocarpus.*
S. fumeus Miller—smoky shrew: *Endogone* spp.; *Glomus macrocarpus.*
S. pacificus: See *Sorex vagrans pacificus.*
S. trowbridgii Baird—Trowbridge's shrew: *Endogone* spp.
S. vagrans Baird—vagrant shrew: *Endogone* spp.
S. vagrans pacificus Coues: fungi.
S. vagrans yaquinae Jackson: *Endogone* spp.
S. yaquinae: see *Sorex vagrans yaquinae.*
FAMILY TALPIDAE
Endogone spp.; fungi.
ORDER PRIMATES
FAMILY CYNOPITHECINAE
Papio cynocephalus L.—yellow baboon: fungi.
ORDER ENDENTATA
FAMILY DASYPODIDAE
Dasypus novemcinctus mexicanus Peters—nine-banded armadillo: Lycoperdales, fungi.
D. novemcinctus texanus: See *Dasypus novemcinctus mexicanus.*
ORDER LAGOMORPHA
FAMILY LEPORIDAE

Amanita rubescens; Castoreum spp.; *Clitocybe brumadis; Elaphomyces granulatus; Hygrophoropsii aurantiaca; Melanogaster ambiguus; Mesophellia* spp.; *M. arenaria; M. pachythrix; Mycena epipterygia; Paxillus involutus; Polyporus betulinus; Sparassis crispa;* Tuberaceae; *Xerocomus badius.*

Lepus europaeus Pallus—brown hare: *Morchella* spp.; fungi.

Oryctolagus cuniculus (L.)—European rabbit: *Helvella* spp., *Lycoperdon* spp., *Marasmius* spp., *Scleroderma* spp.

Sylvilagus palustris paludicola (Miller and Bangs)—marsh rabbit: *Polyporus* spp.

FAMILY OCHOTONIDAE

Ochotona spp.: *Endogone* spp.

O. princeps (Richardson)—pika: *Endogone* spp.; *Glomus fasciculatus.*

ORDER RODENTIA

Amanita muscaria; Boletus edulis; Collybia maculata; Cortinarius collinitus; Elaphomyces granulatus; Hygrophoropsis aurantiaca; Hygrophorus hypothejus; Lactarius necator; L. rufus; Paxillus atrotomentosus; P. involutus; Russula emetica; Suillus bovinus; S. flavidus; S. variegatus; Tuber spp.; *T. aestivum; Xerocomus badius; X. chrysenteron;* fungi.

FAMILY SCIURIDAE

Amanita muscaria; Boletus spp.; *Cronartium ribicola; Elaphomyces granulatus; Hygrophorus pudorinus; Leccinum scabrum; Polyporus* spp.; *Tricholoma flavorvirens;* Tuberaceae.

Callospermophilus spp.: See *Spermophilus* spp.

Citellus spp.: See *Spermophilus* spp.

C. parryii parryii: See *Spermophilus undulatus parryii.*

C. richardsonii: See *Spermophilus richardsonii.*

Eutamias spp.; *Endogone* spp.; fungi.

E. amoenus (J. A. Allen)—yellow-pine chipmunk: Tuberales; hypogeous fungi.

E. cinereicollis cinereicollis (J. A. Allen)—gray-collored chipmunk: fungi.

E. minimus jacksoni: See *E. minimus neglectus.*

E. minimus neglectus (J. A. Allen)—least chipmunk: fungi.

E. minimus pictus (J. A. Allen): fungi.

E. quadrimaculatus (Gray)—long-eared chipmunk: *Boletus* spp.; *Clitocybe* spp.; Tuberales; hypogeous fungi; fungi.

E. quadrivittatus quadrivittatus (Say)—Colorado chipmunk: fungi.

E. speciosus (Merriam)—lodgepole chipmunk: fungi.

E. townsendii (Bachman)—Townsend's chipmunk: Tuberales, hypogeous fungi.

E. townseidii senex (J. A. Allen): fungi.

Glaucomys sabrinus (Shaw)—northern flying squirrel: hypogeous fungi; fungi.

G. sabrinus fuscus Miller: fungi.

G. sabrinus macrotis (Mearns): fungi.

G. volans volans (L.)—southern flying squirrel: fungi.

Pteromys volans: See *Glaucomys volans.*

Sciurus spp.: fungi.

S. aberti aberti Woodhouse—Abert's squirrel: *Agaricus* spp.; *Amanita muscaria; A. vaginata; Boletus* spp.; *Elaphomyces* spp.; *Gautieria* spp.; *Geopora cooperi; Glomus fasiculatus; Hysterangium* spp.; *Lepiota* spp.; *Lycoperdon* spp.; *Martellia* spp.; *Psathyrella* spp.; *Rhizopogon* spp.; *Russula* spp.; *Tuber* spp.; fungi.

S. carolinensis carolinensis Gmelin—eastern gray squirrel: Agaricaceae; *Amanita muscaria; Balsamia vulgaris; Boletus* spp.; *B. calopus; B. impolitus; Collybia maculata; Crepidotus malachias; Daedalea* spp.; *Dibotryon* spp.; *Elaphomyces granulatus; Flammulina velutipes; Hydnum erinaceus; Hygrocybe miniata; Hygrophorous hypothejus; Lactarius deliciosus; Leccinum scabrum; Lycoperdon* spp.; *Melanogaster ambiguus; Paxillus involutus; Pholiota discolor; Pleurotus ostreatus; Pluteus atricapillus; Polyporus* spp.; *P. picipes; P. sulphureus; Russula* spp.; *R. emetica; R. ochroleuca; Stereum hirsutum; Sullus bovinus; Tricholoma terreum;* fungi.

S. carolinensis hypophaeus Merriam: fungi.

S. carolinensis pennsylvanicus Ord.: fungi.

S. cinerus: See *S. carolinensis carolinensis.*

S. douglasii: See *Tamiasciurus douglasii.*

S. fremonti lychnuchus: See *Tamiasciurus hudsonicus lychnuchus.*

S. fremonti mogollonensis: See *Tamiasciurus hudsonicus mogollonensis.*

S. griseus griseus Ord—western gray squirrel: *Gautieria* spp.; *Hysterangium* spp.; *Melanogaster* spp.; Polyporaceae; *Rhizopogon* spp.; hypogeous fungi; fungi.

S. hudsonicus: See *Tamiasciurus hudsonicus hudsonicus.*

S. hudsonicus ventorum: See *Tamiasciurus hudsonicus ventorum.*

S. leucourus: See *Sciurus vulgaris leucourus.*

S. kaibabensis Merriam—Kaibab squirrel: fungi.

S. niger cinereus L.—eastern fox squirrel: fungi.

S. niger neglectus: See *S. niger cinereus.*

S. niger niger L.: Agaricaceae; *Boletus* spp.; *Crepidotus nephrodes; Flammulina velutipes; Hydnum erinaceus; Hygrocybe miniata; Lycoperdon gemmatum; Pholiota discolor; Pluteus atricapillus; Pleurotus* spp.; *P. ostreatus; Polyporus picipes; P. sulphureus;* fungi.

S. niger rufiventer E. Geoffroy St.-Hilaire: fungi.
S. vulgaris (L.)—European red or brown squirrel: *Agaricus campestris; Amanita* spp.; *Armillaria* spp.; *A. mella; Balsamia vulgaris; Boletus edulis; Cantharellus cibarius; Calocera viscosa; Kuehneromyces mutablis; Lactarius torminosus; Leccinum aurantiacum; L. scabrum; Naematoloma fasiculare; Polyporus betulinus; Suillus luteus; Xerocomus;* fungi.
S. vulgaris exalbidus Pallas: *Clitocybe* spp.; *Ganoderma* spp.; *Gomphidius glutinosus; Leccinum aurantiacum; L. scabrum; Pholiota* spp.; *Pluteus nanus; Suillus bovinus; S. luteus; S. piperatus; Xerocomus chrysenteron; X. subtomentosus.*
S. vulgaris leucourus Kerr.: Agaricales; fungi.
S. vulgaris orientis Thomas: fungi.
S. vulgaris varius: See *Sciurus vulgaris.*
Spermophilus spp.: Tuberales; hypogeous fungi; fungi.
S. beecheyi (Richardson)—California ground squirrel: hypogeous fungi; fungi.
S. lateralis (Say)—golden-mantled ground squirrel: *Polyporus* spp.; Tuberales; fungi.
S. lateralis chrysodeirus (Merriam): fungi.
S. richardsonii (Sabine)—Richardson's ground squirrel: fungi.
S. undulatus kennicottii (Ross)—arctic ground squirrel: fungi.
S. undulatus parryii (Richardson): fungi.
Tamias spp.; fungi.
T. striatus fisheri A. H. Howell—eastern chipmunk: Lycoperdaceae; fungi.
T. striatus griseus Mearns: *Geastrum* spp.; fungi.
T. striatus lysteri (Richardson): *Amanita vaginata; Russula* spp.; fungi.
T. striatus striatus (L.): fungi.
Tamiasciurus douglasi albolimbatus (J. A. Allen)—Douglas' squirrel: fungi.
T. douglasi cascadensis: See *T. douglasi mollipilosus.*
T. douglasi douglasi (Bachman): *Alpova diplophloeus; Boletus mirabilis; Gautieria graveolens; Gomphidius rutilus; G. subroseus; Pholiota lenta; Rhizopogon rubescens; R. vinicolor; Russula delica; Suillus granulatus; S. tomentosus; Truncocolumella citrina* var. *citrina;* Tuberales; fungi; hypogeous fungi.
T. douglasi mollipilosus (Aud. and Bachman): fungi.
T. fremonti: See *T. hudsonicus fremonti.*
T. hudsonicus abieticola (A. H. Howell)—red squirrel: fungi.
T. hudsonicus dakotensis (J. A. Allen): fungi.
T. hudsonicus fremonti (Aud. and Bachman): *Polyporus* spp.; *Russula* spp.; fungi.
T. hudsonicus hudsonicus (Erxleben): *Alpova diplophloeus; Amanita* spp.; *A. muscaria; A. phalloides; Amillaria mellea; Boletinus pictus; Boletus* spp.; *B. mirabilis; Cantharellus cibarius; Clitocybe* spp.; *C. brumalis; C. maxima; C. monodelpha; C. odora; Clavicorona pyxidata; Collybia dryophila; C. maculata; Cortinarius* spp.; *C. varius; Elaphomyces granulatus; Fomes fomentarius; F. pinicola; Gautieria graveolens; G. morchelliformis; Gomphidius rutilus; G. subroseus; G. tomentosus; Gomphus floccosus; Gymnopilus sapineus; Gyroporus castaneus; Hericium caput-ursi; Hydnum* spp.; *H. fuligineo-violaceum; H. imbricatum; H. repandum; Hygrophoropsis aurantiaca; Hygrophorus hypothejus; H. pudorinus; Hymenogaster tener; Inocybe* spp.; *Lactarius deliciosus; L. piperatus; L. uvidus; Leccinum scabrum; L. versipellis; Lentinus lepideus; Leucoagaricus naucinus; Lycoperdon pyriforme; Lyophyllum ulmarium; Melanogaster ambiguus; Morchella conica; M. esulenta; Naematoloma fasiculare; Oudemansiella radiacata; Paxillus involutus; Peridermium harknessii; Pholiota carbonaria; Pleurotus ostreatus; Polyporus* spp.; *P. amarus; P. betulinus; Psathyrella* spp.; *Ramaria aurea; R. flava; Rhizopogon luteolus; R. maculatus; R. occidentalis; R. roseolus; R. rubescens; R. viridis; R. vulgaris; Rozites caperata; Russula* spp.; *R. adusta; R. alutacea; R. bicolor; R. blackfordae; R. consobrina; R. decolorans; R. disparilis; R. emetica; R. emetica* ssp. *fragilis; R. mariae; R. nigricans; R. pulchella; R. rosea; R. rosipes; R. xerampelina; Suillus bovinus; S. cavipes; S. granulatus; S. lakei; S. luteus; S. subolivaceus; S. tomentosus; S. variegatus; Tricholoma* spp.; *T. flavovirens; Truncocolumella citrina;* Tuberales; fungi.
T. hudsonicus loquax (Bangs): *Lycoperdon* spp.; *Polyporus* spp.; fungi.
T. hudsonicus lychnuchus (Stone and Rehn): fungi.
T. hudsonicus minnesota (J. A. Allen): *Amanita* spp.; fungi.
T. hudsonicus mogollonensis (Mearns): fungi.
T. hudsonicus preblei A. H. Howell: fungi.
T. hudsonicus richardsoni (Bachman): fungi.
T. hudsonicus streatori (J. A. Allen): fungi.
T. hudsonicus ventorum (J. A. Allen): fungi.
FAMILY GEOMYIDAE
Tuber spp.
FAMILY HETEROMYIDAE
Dipodomys spp.—kangaroo rats: fungi.
Microdipodops spp.—kangaroo mice: fungi.
Perognathus parvus (Peale)—Great Basin pocket mouse: fungi.
FAMILY CASTORIDAE
Castor canadensis Kuhl—beaver: fungi.
FAMILY CRICETIDAE

Endogone spp.
Apodemus sylvaticus (L.)—wood-mouse: *Lycoperdon* spp.; *Paxillus involutus; Xerocomus badius;* fungi.
A. flavicollis Milch.—yellow-necked field mouse: fungi.
Clethrionomys spp.: *Glomus macrocarpus;* fungi.
C. californicus californicus (Merriam)—California red-backed vole: *Endogone flammicorona; E. lactiflua; E. pisiformis; Glomus fasciculatus; G. macrocarpus* var. *macrocarpus; G. microcarpus; G. monosporus; Sclerocystis rubiformis.*
C. gapperi athabascae (Preble)—Gapper's red-backed vole: fungi.
C. gapperi gapperi (Vigors): *Endogone* spp.; *Glomus macrocarpus; Hymenogaster* spp.; *Lactarius lignyotus;* fungi.
C. grapperi paludicola Doutt: fungi.
C. gapperi rhoadsii (Stone): fungi.
C. gapperi rupicola E. L. Poole: fungi.
C. glareolus Schreb.—European bank vole: *Balsamia* spp.; *Genea* spp.; *Hydnotrya* spp.; *Hymenogaster* spp.; *Melanogaster* spp.; *Rhizopogon spp.; Russula* spp.; *Tuber* spp.; fungi.
C. rufocanus Sund.—red-gray vole: fungi.
C. rutilus mikado Thomas—Emperor vole: Boletaceae Russulaceae.
Dicrostonyx groenlandicus (Traill)—Greenland varying lemming: fungi.
D. torquatus Pallas—collared lemming: fungi.
Lagurus curtatus (Cope)—sagebrush vole: *Endogone* spp.; *Glomus fasciculatus.*
Lemmiscus curtatus: See *Lagurus curtatus.*
Lemmus lemmus L.—Norwegian lemming: *Boletus* spp.; *Russula* spp.; fungi.
Microtus agrestis (L.)—North Europe dark vole: fungi.
M. chrotorrhinus (Miller)—rock vole: *Endogone* spp.
M. longicaudus (Merriam)—long-tailed vole: *Endogone* spp.
M. ochrogaster (Wagner)—prairie vole: *Endogone* spp.
M. oeconomus macfarlandi Merriam—tundra vole: *Endogone* spp.; *Hymenogaster* spp.
M. oregoni (Bachman)—Oregon meadow mouse: *Fischerula subcaulis.*
M. pennsylvanicus (Ord)—meadow vole: *Endogone* spp.; *Glomus fasciculatus; Melanogaster variegatus;* fungi.
M. pinetorum (Le Conte)—pine vole: *Endogone* spp.
Neotoma spp.: *Gautieria* spp.; Hymenogastrales; *Hysterangium* spp.; *Melanogaster* spp.; *Tuber rufum* var. *nitidum;* hypogeous fungi.
N. albigula warreni Merriam—white-throated wood rat: Lycoperdaceae.
N. cinerea (Ord)—bushy-tailed wood rat: *Lycoperdon* spp.; fungi; hypogeous fungi.
N. cinerea occidentalis Baird: *Lycoperdon* spp.; fungi.
N. cinerea orolestes Merriam: Agaricaceae; *Polyporus* spp.; fungi.
N. desertorum: See *N. lepida lepida.*
N. floridana attwateri Mearns—eastern wood rat: fungi.
N. floridana floridana (Ord): fungi.
N. floridana magister Baird: Agaricaceae; *Agaricus* spp.; *Boletus* spp.; *B. pallidus; Clavaria* spp.; *Inocybe* spp.; *Lycoperdon* spp.; *Russula* spp.; *Scleroderma citrinum;* fungi.
N. fuscipes annectens Elliot—dusky-footed wood rat: Agaricaceae; Boletaceae; *Elaphomyces* spp.; *Gautieria* spp.; *Hydnangium* spp.; Hymenogastrales; *Hymenogaster* spp.; *Hysterangium* spp.; *Melanogaster* spp.
N. fuscipes fuscipes Baird: *Helvella lacunosa; Melanogaster* spp.; *Morchella conica; Paxina acetabulum; Peziza* spp.; *P. emileia; Pluteus cervinus; Polyporus varius; Scleroderma hypogaeum; Tuber* spp.
N. fuscipes macrotis Thomas: fungi.
N. lepida lepida Thomas—desert wood rat: fungi.
N. magister: See *N. floridana magister.*
N. mexicana fallax Merriam—Mexican wood rat: fungi.
N. pennsylvanica: See *N. floridana magister.*
Onychomys leucogaster (Wied-Neuwied)—northern grasshopper mouse: *Endogone* spp.; *Glomus fasciculatus.*
Oryzomys palustris (Harlan)—marsh rice rat: *Endogone* spp.
Peromyscus spp.: *Glomus macrocarpus.*
P. boylii (Baird)—brush mouse: Tuberales; hypogeous fungi.
P. gossypinus (Le Conte)—cotton mouse: *Endogone* spp.
P. leucopus (Rafinesque)—white-footed mouse: *Endogone* spp.; Uredinales; fungi.
P. leucopus noveboracensis (Fisher): *Endogone* spp.; *Glomus macrocarpus;* fungi.
P. maniculatus (Wagner)—deer mouse: *Endogone* spp.; *E. flammicorona; E. lactiflua; E. pisiformis; Glomus caledonius; G. fasciculatus; G. macrocarpus; G. macrocarpus* var. *macrocarpus; G. microcarpus; Melanogaster variegatus; Sclerocystis rubiformis;* fungi.
P. maniculatus artemisiae (Rhoads): fungi.
P. maniculatus bairdii (Hoy and Kennicott); *Endogone* spp.; fungi.
P. maniculatus gracilis (Le Conte): *Endogone* spp.; fungi.
P. maniculatus osgoodi Mearns: fungi.
P. truei (Shufeldt)—piñon mouse: fungi.

Phenacomys intermedius Merriam—heather vole: *Endogone* spp.
P. intermedius mackenzii Preble: fungi.
P. ungava mackenzii: See *P. intermedius mackenzii.*
Pitymys pinetorum: See *Microtus pinetorum.*
P. subterraneus de Sél.-Long.—European ground vole: fungi.
P. tatricus Kratochvil—Tatra pine vole: fungi.
Synaptomys cooperi cooperi Baird—southern bog lemmings: *Endogone* spp.; *Glomus macrocarpus;* fungi.
S. cooperi gossii (Coues): *Endogone* spp.; *Glomus macrocarpus.*
S. cooperi stonei Rhoads: fungi.
FAMILY MURIDAE
Mastacomys spp.—broad-toothed rats: fungi.
Mus musculus L.—house mouse: *Endogone* spp.
FAMILY ZAPODIDAE
Napaeozapus insignis insignis (Miller)—woodland jumping mouse: *Endogone* spp.; *Hymenogaster* spp.; *Russula* spp.
Zapus hudsonius (Zimmermann)—meadow jumping mouse: *Endogone* spp.; *Hymenogaster* spp.
Z. princeps J. A. Allen—western jumping mouse: *Endogone* spp.; *Glomus fasiculatus; G. pulvinatus.*
Z. trinotatus Rhoads—pacific jumping mouse: *Endogone* spp.; *E. lactiflua; Glomus fasiculatus; G. monosporus; Sclerocystis rubiformis.*
ORDER CARNIVORA
FAMILY MUSTELIDAE
Spilogale spp.: fungi.
S. putorius (L.)—eastern spotted skunk: fungi.

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Larry Basham

and

Lyle Gilbreath

Northwest Fisheries Center
National Marine Fisheries Service
Seattle, Washington 98112

Unusual Occurrence of Pink Salmon (Oncorhynchus gorbuscha) in the Snake River of Southeastern Washington

Abstract

The first positively identified adult pink salmon *(Oncorhynchus gorbuscha)* is reported for the Snake River of Southeastern Washington State. The sightings were in the Tucannon River and at Little Goose and Lower Granite Dams, approximately 625 to 694 km from the Pacific Ocean. Spent female pink salmon carcasses indicated that these fish can migrate long distances and arrive in time to spawn.

Pink salmon *(Oncorhynchus gorbuscha)* of northwestern North America commonly spawn in relatively short coastal streams. In large rivers, they seldom penetrate more than 160 km upstream to spawn (Aro and Shepard, 1967; Atkinson, Rose, and Duncan, 1967; and McPhail and Lindsey, 1970). Neave (1966), however, reported that a substantial segment of the Fraser River pink salmon run travels at least as far upstream as the South Thompson River, about 560 km from the sea.

During the fall of 1975 we observed pink salmon at several locations on the Snake River (a major tributary of the Columbia River) in southeastern Washington State. The most upstream observation was made at river kilometer 694 (Lower Granite Dam), measured from the mouth of the Columbia River.

Although we believe these to be the first sightings of pink salmon in the Snake River drainage, pinks have been counted in the fish ladder at Bonneville Dam on the lower Columbia River as early as 1941 (personal communication with Mr. Ray Oliger, U.S. Army Corps of Engineers, Walla Walla, Washington). At most dams on the Columbia and Snake Rivers, counting stations are operated at some point on the fishway. Salmonids pass over a "counting board" and the counter identifies and tallies a fish instantaneously. Since pink salmon are rare upstream from Bonneville Dam, fish counters are not expected to recognize an incidental run. Therefore, when a pink escapement larger than expected occurred in 1975, some dam counts showed pinks, whereas others did not. Probably the total run was greater than recorded. At any rate, counts in 1975 were: Bonneville Dam—309; The Dalles Dam—0; John Day Dam—45; McNary Dam—0; Ice Harbor Dam—0; Lower Monumental Dam—0; Little Goose Dam—12; and Lower Granite Dam—0. We made an independent observation at Lower Granite Dam (one fish).

The National Marine Fisheries Service (NMFS) operates trapping facilities for adult salmon and steelhead trout *(Salmo gairdneri)* at Little Goose and Lower Granite

Figure 1. The lower Snake River and locations where pink salmon were observed.

Dams on the lower Snake River (Fig. 1). On September 24, 1975, a male pink salmon 559 mm long weighing 1.6 kg was captured at Little Goose Dam. The external characteristics we used for identification included: a large hump with a very thin keel; extremely small scales; spots on both lobes of the caudal fin, spots larger than the pupil of the eye; yellow and pink coloration below the lateral line. In early October, a female pink salmon was captured at Little Goose Dam and a male pink salmon was captured at Lower Granite Dam 60 km upstream of Little Goose Dam.

During the fall of 1975, routine spawning ground surveys were made for fall chinook salmon *(Oncorhynchus tshawytscha)* spawning in the lower Tucannon River, a small tributary of the Snake River near Starbuck, Washington (about 625 km from the Pacific Ocean). Five pink salmon carcasses were recovered on these surveys: one on October 18, three on October 25, and one on November 1. One of the carcasses was sent to Dr. Richard L. Wallace, Associate Professor of Zoology at the University of Idaho, for species verification. He determined that it was a spent female pink salmon

573 mm in length. The following characters were used in the identification: gill rakers—12 upper and 19 lower; pored scales in lateral line—167; scales in first row above lateral line—203; pyloric caeca—173. This specimen was added to the collection of the Department of Biological Sciences at the University of Idaho.

The four carcasses of female pink salmon recovered from the lower Tucannon River contained only a few eggs and their caudal fins were frayed as if from redd building. Although the redds we observed could not be positively identified as those of pink salmon (spawning fall chinook salmon were present), the observations indicate that pink salmon can reach the lower Snake River area in time and in condition to spawn successfully.

Contacts with fishery agencies of Washington, Oregon, and Idaho have revealed no known attempts to establish pink salmon in the Snake River drainage. The fish may be remnants of a small Columbia River stock which may now be entering the Snake River system. It is unlikely that they are strays from a short-run costal stock. However, they could be strays from long-run stocks such as those from the Frazier River system.

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Ronald J. Taylor

Biology Department
Western Washington University
Bellingham, Washington 98225

and

George W. Douglas

Douglas Ecological Consultants Ltd.
207-737 Fort Street
Victoria, B.C., Canada

Plant Ecology and Natural History of Chowder Ridge, Mt. Baker: A Potential Alpine Research Natural Area in the Western North Cascades

Abstract

The natural history of Chowder Ridge is of particular interest for several reasons: (1) Chowder Ridge contains the largest area of continuous alpine vegetation in the western North Cascades. The area is especially impressive if considered jointly with the adjacent northwest-southeast section of Skyline Divide. (2) Because of the southwest aspect of Chowder Ridge, water stresses are more critical than those typifying the North Cascades in general. This fact results in a curious mixture of relatively drought-tolerant plants more frequently encountered in the eastern Cascades and Rocky Mountains with the characteristic species of the western North Cascades. (3) Chowder Ridge contains all the landforms characteristically associated with the alpine zone, e.g., frost heaving, rock stripes, soil stripes, vegetation stripes, turf-banked terraces, turf-banked lobes, massive solifluction, coarse talus, extensive fell-fields, and sparsely vegetated rock formations. (4) Chowder Ridge is of sedimentary origin whereas associated mountain formations are composed primarily of andesite. (5) Chowder Ridge remains more or less undisturbed by man; thus the flora and fauna have remained in a relatively natural state. Because of this unique combination of physical and biological characteristics, the Chowder Ridge area is incomparably suited for Research Natural Area designation.

Introduction

Until the recent work of Douglas (1971, 1972, 1973) and Douglas and Bliss (1977), botanical studies in the North Cascades in general and the Mt. Baker area in particular were restricted in number and limited in scope, including floristic descriptions (Gorman, 1907; St. John and Hardin, 1929; Muenscher, 1941; Douglas and Taylor, 1970; Taylor *et al.*, 1973) and regional community analyses (Franklin and Dyrness, 1969; Franklin and Trappe, 1963). However, with the work of Douglas (especially 1973) and extensive collecting by the authors, it is now possible to evaluate the Chowder Ridge area (including the adjacent northwest-southeast section of Skyline Divide) with respect to other alpine areas in the western North Cascades. From this evaluation, we are convinced that the Chowder Ridge area should be incorporated into the Research Natural Area (RNA) system of the Pacific Northwest as the principal alpine representative of the western North Cascades. At the present time there is no representation of an "alpine community mosaic with krummholz tree groups" in the western North Cascades (Dyrness *et al.*, 1975). The Chowder Ridge area is the ideal candidate to fill this need.

Research Natural Areas are natural ecological reserves which were defined by Dyrness *et al.* (1975) as "naturally occurring physical or biological units where natural conditions are maintained insofar as possible." The Federal Committee on Research Natural Areas (1968) described the objectives of the RNA system as follows: (1) preservation of examples of all significant natural ecosystems for comparison with those influenced by man; (2) provision of educational and research areas for ecological and environmental studies; (3) preservation of gene pools for typical and rare and endangered plants and animals. A fourth very important objective would seem to be the study of evolutionary processes, especially unique adaptations of plants and animals. This justification for establishment of RNAs in addition to national parks, wilderness areas, etc., is that the latter land-use classification types are dedicated to conservation and/or recreation, not research and education. It is fortunate that the Chowder Ridge area occurs within the Mt. Baker National Forest inasmuch as the forest service is dedicated to the RNA system and has established a major objective of representing as many of the natural plant community types as possible (Romancier, 1974).

Description of the Chowder Ridge Area

Chowder Ridge is located in the Mt. Baker National Forest, within Township 38N and Range 7E. The ridge crest is approximately 5 km long and is oriented from northwest, as a continuation of Skyline Divide, to southeast, running into Bastile Ridge and Mazama Glacier of Mt. Baker (Fig. 1). Elevation varies from 2,031 m (just above Skyline Divide) to 2,312 m at the highest point, with a mean approximately 2,154 m. Both the southwest and northeast slopes are steep (approximately 45 percent), the latter being covered by late-melting snow or ice fields.

The weather of Chowder Ridge is variable and often severe. The prevailing winds follow the general pattern for that of the North Cascades, northwesterly during spring and summer and southwesterly during fall and winter (Douglas, 1972). The nearest meteorological data are recorded from the Mt. Baker station (1,296 m). At that site, the mean annual precipitation is 2,790 mm with only 274 mm occurring during the summer months (June, July, and August). The mean annual temperature is 4.4C with a July mean of 12.1C.

Geologic History

The Mt. Baker area is characterized by landforms caused by sedimentation, uplift, volcanics, and glaciation. The oldest rocks in the area belong to the Yellow Aster complex. Basement rocks are made up of the Shuksan Group metamorphics, Chilliwack Group sediments and volcanics, and the Nooksack Group sediments (Easterbrook and Rahm, 1970). Mt. Baker itself is a composite volcano made of alternating layers of lava and pyroclastic materials.

The ruggedness of the area is due in large part to the action of alpine glaciers which reached their maximum development during the Pleistocene Ice Age and again as recently as 500 years ago. Alpine glaciers were overrun below about 1,700 m by continental ice sheets, the last (Fraser Glaciation) receding 10,000 years ago (Easterbrook and Rahm, 1970). At present the alpine glaciers fluctuate in size as a consequence of temperature variations and snow accumulation.

According to Misch (1966), most of Chowder Ridge is of sedimentary origin,

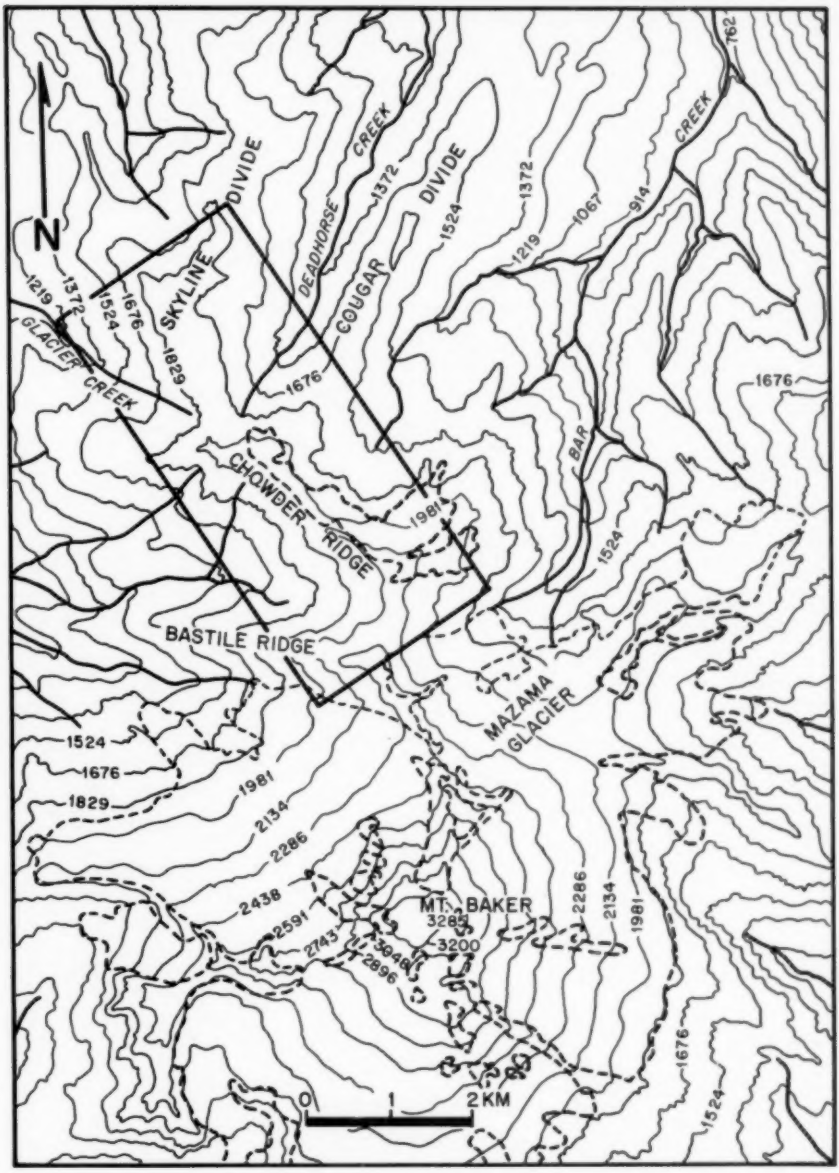

Figure 1. Map of Chowder Ridge and surrounding area. Elevation is given in meters with topographic lines separated by approximately 152 m (500 ft). The area enclosed within the rectangle is proposed as an alpine research natural area.

of the Nooksack Group. This group is of late Jurassic and early Cretaceous age and consists of graywackes, siltstones, granite rocks, and limestone boulders. The group is fossiliferous and appears to have been formed during a period of rapid marine accumulation. The marine fossils are responsible for the name "Chowder Ridge." Uplift and deformation of the sedimentary rocks is shown by folded, sometimes nearly vertical beds. The ridge itself appears to be an arete formed by Pleistocene alpine glaciers. Glacial remnants are seen along the northeast slope, especially in the area where Chowder joins Bastile Ridge. Here the Chowder Glacier abuts against the northwest lobe of Mazama Glacier (see Fig. 1).

Weathering and erosion have been dominant factors in shaping Chowder Ridge and in establishing superficial landforms. Extensive deposits of pebbles and boulder-size sediments funnel into the three principal streams containing runoff water from the ridge. These streams, Bar Creek, Deadhorse Creek, and Glacier Creek, eventually empty into the north fork of the Nooksack River.

The sedimentary origin of Chowder Ridge is an unusual and interesting feature. Other mountain formations immediately associated with Chowder Ridge are apparently composed primarily of andesite. These include Skyline Divide, Cougar Divide, Bastile Ridge, and Mt. Baker itself.

Predominant Animal-Life

The most conspicuous animals of Chowder Ridge are mountain goats which graze the south slopes during the summer but apparently spend the winter on better protected ridges such as Barometer Mountain in the Wells Creek area. The most common inhabitants, however, are rodents, several species of which are known to occur on Chowder Ridge or may be expected to live there given their distribution on adjacent Cougar and Skyline Divides. The largest and most obvious of these is the hoary marmot *(Marmota caligata)* which frequents both the northern and southern slopes of Chowder Ridge, building its den near or below snowfields. Here water-release continues through the summer, providing an abundance of vegetation for the herbivorous marmot. Pikas *(Ochotona princeps)* are common on Cougar Ridge and may be expected in suitable rock formations on Chowder. Unlike the marmot which hibernates, the pika remains active through the winter, feeding on "hay piles" stored during summer. One of the most common rodents of mountain meadows in the Mt. Baker area is the heather vole *(Phenacomys intermedius)*. As the name suggests, this mouse is normally found in heather meadows where it remains active through the winter, building nests of grasses and sedges beneath the snow and heather. It excavates rather extensive tunnel and room systems under the snow and feeds on nearby vegetation. As the snow melts, the nests and latrine piles are readily seen scattered over the meadows. The water rat *(Microtus richardsonii)* also builds nests and tunnel systems under the snow, but usually not in heather communities. The tunnels are often earth-filled and as the snow melts they appear as shallow elongate mounds, often several meters long, or rutted runways through the vegetation. Two other mice of the area are the forest deer mouse *(Peromyscus oreas)* and the Pacific jumping mouse *(Zapus trinotatus)*, the latter hibernating during the winter. Mice are most prevalent in the subalpine zone, on the north slope of Chowder near Cougar Divide. The upper south slopes are used most extensively in early summer. As the alpine meadows become dry in the summer, the mice migrate

downward, returning in early fall. Chipmunks *(Eutamias townsendi)* are common inhabitants of subalpine areas, especially among tree clumps. Occasionally they also range upward into the alpine zone.

Carnivores of Chowder include such transient hunters as the cougar and coyote. The wolverine has also been reported to be in the area (Senger, pers. com.). The insectivorous dusky shrew *(Sorex obscurus)* is a frequent inhabitant of the area and is active all winter. Finally, deer and bear may be expected in the subalpine areas of both the north and south slopes.

Although no attempt has been made to inventory the birds of Chowder Ridge, two species deserve mention. These are blue grouse *(Dendrogapus obscurus)* of subalpine habitats, and ptarmigan *(Lagopus leucurus)*, a common inhabitant of the rugged alpine slopes.

Vegetation: Method of Analysis

The quantitative data presented in this paper are part of a more extensive study involving alpine plant communities of the North Cascades Range (Douglas, 1973; Douglas and Bliss, 1977). In that study fifteen stands were quantitatively sampled in the alpine zone of Chowder Ridge and subalpine stands were qualitatively described. Determinations of vegetative patterns have been based on these analyses plus additional observations by the authors.

The term "stand" refers to a particular example of homogeneous vegetation which was sampled. "Community" or "community type" is a grouping of similar stands. Each stand was quantitatively sampled with twenty 20 x 50 cm quadrats set out (perpendicular to the slope contours) by a restricted random technique (Bliss, 1963) in a 5 x 10 m area. Crown cover, using the methods and cover classes of Daubenmire (1959, 1968), was estimated for all vascular plant species in each quadrat. Frequency and average cover for each species were calculated and converted to prominence values by multiplying the average percentage cover by the square root of the species frequency in each stand, a modification of the procedure used by Beals (1960). This index provides a technique by which cover and frequency may be combined into a single value for use in mathematical equations and in constructing shorter and more easily interpreted tables (see Fig. 2).

Similarity coefficients (C) between stands were then computed using the formula $C = 2w/(a+b) \times 100$ (Gleason, 1920). In this formula, w is the sum of the lowest prominence values of species common to both stands, and a and b are the total prominence values of all species in stands a and b. Species were not adjusted in relation to their maximum values of frequency and cover. Dissimilarity values $(1-C)$ were then computed and used for the construction of two-dimensional ordinations following Bray and Curtis (1957) and Beals (1960). The ordinations allowed the groupings of stands into community types that are correlated with several environmental gradients.

Results and Discussion

Zonal Patterns—The vegetative zones on Chowder Ridge were shown to be distinct and readily recognizable. The montane zone or closed forest ends abruptly at approximately 1,500 m and is more or less restricted by the topography to the western end of the ridge. Because of prominent snowfields and glaciers on the northern slopes, the

subalpine zone[1] is restricted to the south side and western end of the ridge. Even here, the subalpine vegetation is limited to a narrow band, probably because of the steep (approximately 45 percent) slope and prevailing aspect, resulting in less snow accumulation, earlier snowmelt, and more rapid runoff. The resulting xeric conditions are more favorable to alpine vegetation. Because of these factors, the alpine zone is very extensive and comprises the greater part of the vegetation on Chowder Ridge.

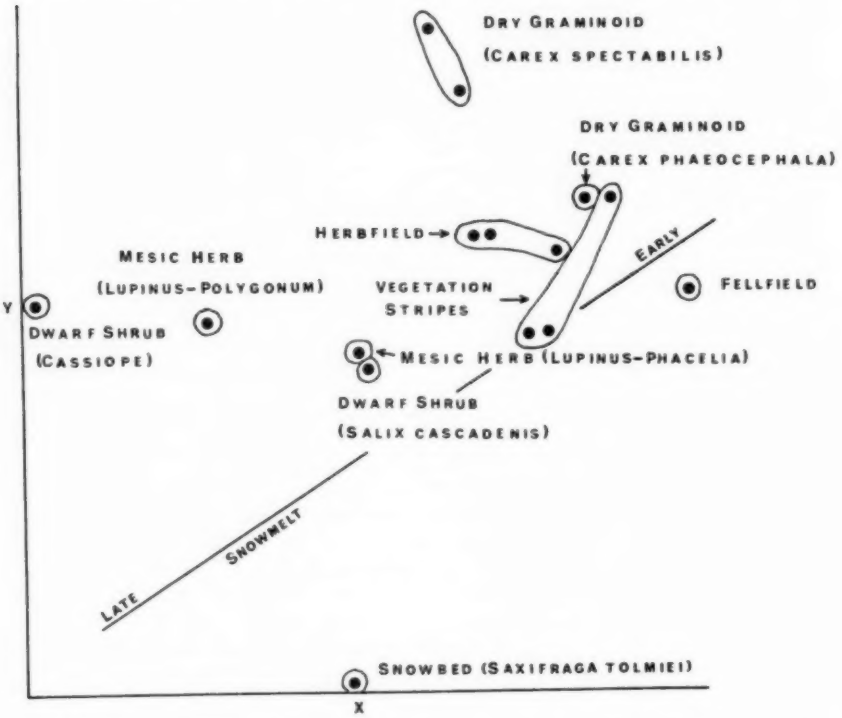

Figure 2. Ordination of 15 stands sampled in the alpine zone on Chowder Ridge, Mt. Baker. Lines delimit community types whose names, where appropriate, are derived from the dominant species.

Community Patterns—The major plant communities in the subalpine and alpine zones of Chowder Ridge are usually sharply delineated and create a complex mosaic over the landscape. This patterning of communities is a response to various environmental parameters, especially wind amount (and its influence on evapotranspiration), snow depth, and time of snowmelt. According to Bliss (1969, 1971), these factors are the most important in determining plant community structure at high elevations throughout western North America.

[1] The subalpine zone is defined here as that area above the montane (closed) forest and below the upper limit of conifers as an upright tree form. Above this is the alpine zone where tree species occur only in a dwarfed or krummholz form (Douglas, 1972, 1973, 1974; Douglas and Bliss, 1977).

Plant Community Types—Eight community types were recognized in the subalpine and alpine zones of Chowder Ridge. Six of these represent habitat-physiognomic types whereas the other two (fell-fields and vegetation stripes) are associated with patterned ground. The vegetational composition and structure and the topographic characteristics of these community types are described below.

Subalpine Zone

Mesic Herb Communities—These communities are dominated by herbs 10 to 40 cm tall and occur on moist, fairly well to well-drained sites. On steep slopes where snowmelt is earlier, *Carex spectabilis* forms a lush, dominant cover. Important associates are *Lupinus latifolius* var. *subalpinus* and *Polygonum bistortoides*. On more moderate slopes where snow accumulation is greater, *Luetkea pectinata* is the dominant species. A number of other species are also of importance on these latter sites. Some of these species are *Deschampsia atropurpurea* var. *latifolia, Carex spectabilis, Castilleja parviflora* var. *albida,* and *Hieracium gracile* var. *gracile.*

Dwarf Shrub Communities—This community type is characterized by low (10 to 30 cm) ericads and occurs on the more mesic slopes or sporadically along the lower flanks of the ridge. These communities may be dominated by either *Cassiope mertensiana* and *Phyllodoce empetriformis* or *Vaccinium deliciosum*. In stands where *Cassiope* and *Phyllodoce* dominate, *Vaccinium deliciosum* and *Luetkea pectinata* are conspicuous components. Where *Vaccinium deliciosum* is the major species, *Phyllodoce empetriformis* and *Luetkea pectinata* are also important elements. The ecological differences associated with this change in floristic composition is not well known, although the *Vaccinium* dominated stands are more often, but not exclusively, found in close proximity to subalpine tree clumps (Douglas, 1972).

Snowbed Communities—In depressions or on gentle slopes where snow accumulates and persists until mid- or late summer, *Carex nigricans* forms a continuous mat of vegetation. Frequent associates of *C. nigricans* in these snowbed communities are *Epilobium alpinum* var. *alpinum* and *Luetkea pectinata,* both with low cover values.

Tree Clump Communities—On Chowder Ridge, tree clumps, although conspicuous, are restricted to a relatively limited band along the southwest to west flanks of the ridge. These stands are found on mesic mounds or ridges which are the first areas to become snow free in the subalpine zone. They are dominated mainly by *Tsuga mertensiana* and *Abies amabilis* with occasional occurrences of *Abies lasiocarpa* and *Chamaecyparis nootkatensis*. The understory of these tree clumps is variable depending on density. In open stands, *Vaccinium membranaceum, A. amabilis, T. mertensiana,* and *Phyllodoce empetriformis* are common while in closed stands understory vegetation is sparse. On the periphery of most clumps a band of tall shrubs (e.g., *V. membranaceum, Rhododendron albiflorum, Sorbus sitchensis* var. *grayi*) is generally present. This peripheral vegetation is probably a response to the more favorable microenvironment provided by the tree clump (Douglas, 1972).

Alpine Area

Since quantitative data are available for most of the alpine community types, an ordination illustrating the floristic relationships of the stands has been constructed (Fig. 2). The stand groupings or community types are correlated with particular environmental

factors, the most obvious of which are time of snowmelt and subsequent moisture availability.

Mesic Herb Communities—At lower elevations in the alpine zone, where snow persists slightly longer, the steep slopes are dominated by a lush herbaceous cover. These sites remain moist throughout much of the growing season due to melting of snowbanks upslope. *Lupinus latifolius* var. *subalpinus* is the most prominent species in these stands (Table 1). Other important plants are *Polygonum bistortoides, Vaccinium*

TABLE 1. Composition of alpine plant community types on Chowder Ridge, Mt. Baker. Data are for prominence value indices.[a]

	Community Types									
Species	S-ST[b] (1)[c]	DS-CM (1)	DS-SC (1)	MH-LP (1)	MH-LPh (1)	DG-CP (1)	DG-CS (2)	HF (3)	VS (3)	FF (1)
Saxifraga tolmiei	226									
Juncus drummondii var. subtriflorus	27									
Luzula piperi	26		16	37						
Carex nigricans	14	8		6						
Carex spectabilis	2	44	20	105		5	533			
Cassiope mertensiana		369								
Vaccinium deliciosum		320		249						
Phyllodoce glanduliflora		296								
Luetkea pectinata		286		136						
Sibbaldia procumbens		5				14	80			
Hieracium gracile		5		40						
Polygonum bistortoides		4		389						
Deschampsia atropurpurea		4		79						
Potentilla flabellifolia		T								
Salix cascadensis			324							
Festuca ovina var. brevifolia			8			41	40		14	10
Luzula spicata			3			18	6	4	4	
Penstemon procerus var. tolmiei			2	3			2		T	
Antennaria umbrinella			1				17	1		
Lupinus latifolius var. subalpinus				865	598					
Trisetum spicatum				14			T	16	3	T
Erigeron peregrinus var. scaposus				12						
Poa cusickii var. purpurescens				10						
Arnica latifolia var. gracilis				8						
Phlox diffusa var. longistyla				6		160	155	250	36	85
Carex rossii				6						
Phacelia heterophylla var. pseudohispida					57					
Epilobium alpinum var. lactiflorum					2					
Poa cusickii var. epilis					2					
Carex phaeocephala						236	3	49	5	34
Solidago multiradiata var. scopulorum						96	125	141	37	33
Oxytropis campestris var. gracilis						94		147	36	50
Carex breweri var. paddoensis						36	134			
Selaginella densa						36	2	48	7	51

TABLE 1. (Continued)

Potentilla diversifolia	31	4	232	8	4
Haplopappus lyalli	18		2		
Campanula rotundifolia	2	2	1	1	4
Cerastium arvense	1	1	52	25	2
Sedum lanceolatum	1	2	13	2	
Antennaria alpina var. media		42		9	
Lupinus lepidus var. lobbii		10		2	
Achillea millefolium ssp. lanulosa var. alpicola		1	74	9	
Veronica cusickii	1				
Agrostis scabra		T			6
Carex albonigra			97	8	
Poa alpina			62	7	
Antennaria rosea			17		
Draba praealta			8	T	
Silene acaulis var. escapa			4	15	
Draba lonchocarpa			1	T	
Potentilla fruticosa			1	2	
Phacelia sericea			1	7	1
Saxifraga occidentalis			1		
Draba incerta			1	2	
Silene parryi			T		
Agropyron caninum var. latiglume				10	
Castilleja rupicola				4	
Erigeron compositus var. glabratus				3	
Potentilla villosa var. parvifolia				1	18
Taraxacum ceratophorum				1	
Arenaria rubella				T	
Stellaria longipes var. altocaulis				T	
Saxifraga bronchialis var. austromontana					3

[a] T (trace) indicates a prominence value of less than 0.5.

[b] Abbreviations for community types and dominant species: S-ST = Snowbed—*Saxifraga tolmiei;* DS-CM = Dwarf shrub—*Cassiope mertensiana;* DS-SC = Dwarf shrub—*Salix cascadensis;* MH-LP = Mesic herb—*Lupinus latifolius—Polygonum bistortoides;* MH-LPh = Mesic herb—*Lupinus latifolius—Phacelia heterophylla;* DG-CP = Dry graminoid—*Carex phaeocephala;* DG-CS = Dry graminoid—*Carex spectabilis;* HF = Herbfield; VS = Vegetation stripes; FF = Fell-field.

[c] Number of stands sampled appears in parentheses.

deliciosum, Luetkea pectinata, and *Carex spectabilis.* The abundance of subalpine elements in these stands indicates their close relationship with subalpine vegetation.

A second alpine mesic herb type occurs locally along the flanks of the ridge between approximately 2,030 and 2,090 m elevation. This band, about 100 m long, occurs on a steep, relatively unstable slope. Species richness is low, with only *Lupinus latifolius* var. *subalpinus* being important (Table 1). Other species present are *Phacelia heterophylla* var. *pseudohispida, Epilobium alpinum* var. *lactiflorum,* and *Poa cusickii* var. *epilis.*

Dry Graminoid Communities—On some of the well-drained, exposed upper slopes and ridgetops, where snow cover melts by early summer, floristically rich communities dominated by sedges are found. The most extensive community of this type is dominated by *Carex spectabilis* (Table 1). These alpine *C. spectabilis* stands are markedly different from those of the subalpine zone. The drier alpine stands are not only richer floristically

but are characterized by prominent alpine elements such as *Phlox diffusa* var. *longistylis, Carex breweri, Sibbaldia procumbens, Solidago multiradiata* var. *scopulorum, Antennaria aplina* var. *media,* and *Festuca ovina* var. *brevifolia.*

The most xeric sites occupied by dry graminoid communities are dominated by *Carex phaeocephala* with important associates including *P. diffusa* var. *longistylis, S. multiradiata* var. *scopulorum,* and *Oxytropis camestris* var. *gracilis* (Table 1).

Dwarf Shrub Communities—Two dwarf shrub communities occur in the alpine zone on Chowder Ridge. The most common is the heath type which has close floristic affinities with the subalpine heath type. In the alpine communities, however, *Phyllodoce empetriformis* is mostly replaced by *P. glanduliflora* and is co-dominant with *Vaccinium deliciosum, Cassiope mertensiana,* and *Luetkea pectinata* (Table 1). Except for the increased elevation and the occurrence of these stands above tree-line, the ecological differences are not readily apparent.

Several small stands dominated by *Salix cascadensis* occur near the crest of the ridge. These nearly pure mats occur in slight depressions (Table 1).

Snowbed Communities—Flat boulder fields are prominent on the eastern end of Chowder Ridge, along the southern flank. Snow accumulates in these sites, resulting in a short growing season. Here vegetative cover is sparse with only *Saxifraga tolmiei* var. *tolmiei* being common in spaces between the boulders (Table 1). Less frequent associates include *Juncus drummondii* var. *subtriflorus* and *Luzula piperi.*

Herb-field Communities—Continuous vegetation comprised of a rich assemblage of plants with a cushion or matted habit occurs on many of the exposed ridgetops. Most of these stands cover a limited area. Some of the more prominent species on these sites are *Phlox diffusa* var. *longistyla, Potentilla diversifolia, Oxytropis campestris* var. *gracilis, Solidago multiradiata, Carex albonigra, Achillea millefolium,* and *Poa alpina* (Table 1).

Fell-field Communities—These sparsely vegetated communities are restricted to relatively level sites along the ridgetop. The plants are scattered, usually in clumps, among the frost-shattered rocks. Characteristic species, with low cover values, are *Phlox diffusa* var. *longistyla, Selaginella densa, Oxytropis campestris* var. *gracilis, Carex phaeocephala, Solidago multiradiata* var. *scopulorum,* and *Saxifraga bronchialis* var. *austromontana* (Table 1).

Vegetation Stripe Communities—Along the south-facing flank of the ridge, on the upper slopes near the ridge tops, the vegetation is arranged in long stripes 20 to 40 cm wide, each separated by about 1 m of scree material. This striping is a result of the downslope creep of the unstable substrate. Floristically, the composition of these communities is similar to that found in the fell-fields (Table 1). Some of the more common species in the vegetation stripes are *Solidago multiradiata* var. *scopulorum, Phlox diffusa* var. *longistyla, Oxytropis campestris* var. *gracilis, Cerastium arvense, Silene acaulis* var. *escapa,* and *Festuca ovina* var. *brevifolia.*

Krummholz Communities—In the lower part of the alpine zone, along the southern flanks of the ridge, clumps of dwarfed tree species (krummholz) occur. Because of their ability to accumulate snow, these stands become snow free later than all other communities except those of snowbeds. *Abies lasiocarpa* is the dominant species with *Tsuga mertensiana* occurring infrequently. Understory vegetation is usually sparse or lacking.

Floristics

Several factors have contributed to the interesting nature of the floristics of the Chowder Ridge area. The area has contrasting habitats, especially those associated with steep, dry, southerly slopes and those of cool, snowy, equally steep north slopes. The climatic conditions of the south slopes resemble those of the eastern Cascades and northern Rockies, resulting in an unusual mixture of relatively drought-tolerant species. Finally, the Chowder Ridge area is located at the southern limit of glaciation, with consequential representation of northern and southern species. These and other features contribute to the floristic diversity and species richness of the area.

The species of the area can for convenience be divided into three major categories: (1) typical representatives of the western North Cascades; (2) species typically occurring in the eastern Cascades and northern Rockies; (3) plants representing range extensions of more northerly distributed species. These categories, especially the latter two, are not clearly distinct. The first group is naturally the largest and includes most of the dominants of the area, which as such are discussed in the plant communities section of this paper. The second group includes several species, the most notable of which are briefly discussed below. The general range of such species is cited from Hitchcock *et al.* (1955-1969).

Arnica rydbergii—This is an uncommon plant on Chowder Ridge and has rarely been collected at other locations in the North Cascades (Taylor *et al.*, 1973). It is generally found in the northern Rockies and eastern Cascades, extending south into California.

Astragalus alpinus—This is a circumpolar species which is common in the alpine zone of the Rocky Mountains. It is well known from the eastern Cascades but has rarely been collected west of the Cascade crest. It is an occasional plant on Chowder Ridge.

Carex breweri var. *paddoenis*—This species is fairly common on Chowder Ridge and has frequently been collected by the authors at other locations in the western North Cascades (Taylor *et al.*, 1973). Previously it was thought to be restricted to the eastern Cascades and Rocky Mountains.

Carex capitata—This is a circumboreal species which is common throughout much of the Rocky Mountains, extending west to the Sierra Nevadas of California. Prior to collections by the authors (Taylor *et al.*, 1973), this sedge was not known from Washington, and Chowder Ridge is the only location where it is known to occur west of the Cascade crest.

Carex nardina—This is another circumboreal sedge which is widespread in the Rocky Mountains. Collections by the authors indicate a rather broad range for this species in the North Cascades, including Chowder Ridge (Taylor *et al.*, 1973).

Draba ventosa var. *ruaxes*—*Draba ventosa* is chiefly a Rocky Mountain taxon and the var. *ruaxes* is known only from a few collections from the Glacier Peak area (Taylor *et al.*, 1973) and Chowder Ridge.

Eriogonum umbellatum—This desert buckwheat is extremely common in the Rocky Mountain area and Great Basin plains. It occasionally occurs in the eastern Cascades but seldom on the west side (especially in the North Cascades). Both *E. umbellatum* var. *subalpinum* and var. *hausknechtii* occur in the Chowder Ridge area.

Poa rupicola—This bluegrass is common throughout much of the Rocky Mountains but was not known to occur in the Cascades until 1970 (Douglas and Taylor, 1970).

It has now been collected at two locations in the North Cascades, Chowder Ridge and Hoodoo Pass, Chelan County (Taylor *et al.*, 1973).

Salix nivalis—This dwarf apline willow is known to occur at several locations in the North Cascades, including the Chowder Ridge area. However, it is much more prevalent in the high mountains of the Rockies.

Vaccinium occidentale—This species of huckleberry or blueberry is fairly common in the northern Rocky Mountains and is well known on the east side of the Cascades; however, it has rarely been collected west of the Cascade crest. In the Chowder Ridge area (SE end of Skyline Divide) it is a local dominant on a windswept plateau (Taylor *et al.*, 1973).

Vaccinium scoparium—Grouseberry is a very common species in the understory of coniferous forests in the eastern Cascades and especially in the Rocky Mountains where it occasionally extends upward into the alpine zone. The Chowder Ridge area is the only location where this species is known to occur west of the Cascade crest.

The third floristic group is smaller and cannot easily be distinguished from the previous group in that representative species may occur in the northern Rockies. However, species of the third group are generally associated with tundra environments of northern Canada and Alaska. This group constitutes an interesting part of the Chowder Ridge area flora. The most notable species are listed and briefly discussed below.

Aster sibiricus—This is a circumboreal species, extending southward in the northern Rockies as well as in the Cascades. However, the southern limit of its distribution in the Cascade Range appears to be the Mount Baker area. It is fairly common on Chowder Ridge.

Empetrum nigrum—This species is by no means restricted in the Cascades to the Chowder Ridge area, but it is an important cushion plant there. It achieves its best development in the arctic-alpine tundra of northern Canada and Alaska.

Gentiana glauca—This small gentian is common in the tundra of northern Canada and Alaska. In Washington, it has now been collected at two locations, the Chowder Ridge area (SE Skyline Divide) and Horseshoe Mt. in Okanogan County (Douglas and Taylor, 1970; Taylor *et al.*, 1973).

Lycopodium alpinum—This is an attractive and distinctive circumboreal clubmoss which has extended southward along mountain ranges. In the Cascades it reaches Washington where it is known to occur at only a few sites, one the Chowder Ridge area (Taylor *et al.*, 1973).

Saxifraga oppositifolia—This is a rare alpine plant in the North Cascades, being known from only a few locations including Chowder Ridge. It is well known, however, in more northern environments, the northern Rockies, and northeastern North America.

A few species occurring in the Chowder Ridge area are at or near the northern limit of their distribution; for example, *Arnica nevadensis*, primarily of the Sierras. Other unusual plants are rare color variants of common alpine species. These include white-flowered forms of both *Lupinus lepidus* var. *lobbii*, and *Silene acaulis*. The yellow-flowered variant of *Claytonia lanceolata* (previously *C. lanceolata* var. *chrysantha*, see Douglas and Taylor, 1972) occurs in a local population at the SE end of Skyline Divide. Finally, a number of relatively uncommon, typically Cascade plants are scattered over the Chowder Ridge area.

Although the moss flora of Chowder Ridge has not been systematically studied,

there is little doubt that a careful inventory would yield "unusual" species. For example, *Poblia erecta,* previously known in western North America from only two collections, one from Mount Rainier and the other from the British Columbia Cascades (W. B. Schofield, pers. comm.), has been collected[2] in a fell-field community along the ridge crest.

Plant collections taken by the authors from the Chowder Ridge area (including Chowder Ridge and the northwest-southeast segment of Skyline Divide) are alphabetically listed in Table 2.

TABLE 2. Plant collections from the Chowder Ridge area.[a]

Achillea millefolium lanulosa alpicola—D 2239, T 1270
Agoseris aurantiaca aurantiaca—D 2253, DD 4375
Agropyron caninum majus latiglume—D 2241, D 2278, T 1274, T 2589
Agrostis idahoensis—T 2184
A. scabra—T 1277, T 2610
Androsace septentrionalis subumbellata—D 2305, T 4322
Anemone drummondii—T 1662
A. multifida hirsuta—T 2609
A. multifida multifida—D 2276, T 728
Antennaria alpina media—D 2244, D 2407, DD 4289, DD 4312, T 3122, T 3145
A. microphylla—D 2306, D 4255, DD 4370, T 3524
A. umbrinella—D 4305a, DD 4356
Arabis lyallii—D 2330, T 1643, T 1647
Arenaria nuttallii—T 1659
A. obtusiloba—D 2331
A. rubella—T 3534
Arnica latifolia gracilis—DD 4373
A. nevadensis—T 3531
A. rydbergii—T 3532
Aster foliaceous foliaceous—DD 4374
A. sibiricus meritus—D 2251, DD 4346, T 743
Astragalus alpinus—T 1663
Campanula rotundifolia—D 2242, T 751
Cardamine oligosperma kamtschatica—D 4271 (specimen not retained)
Carex albonigra—D 2237, DD 4349, T 1909
C. breweri paddoensis—T 3526
Carex capitata—DD 4285, DD 4345
C. nardina—DD 4335
C. nigricans—D 2270, T 1280, T 2602
C. phaeocephala—D 2245, D 2289, DD 4355, T 1281, T 1284, T 2587
C. pyrenaica—D 2262, T 1281
C. rossii—D 2265
C. spectabilis—D 2271, D 2408, T 1283, T 2601
Cassiope mertensiana—T 3142, T 5213
Castilleja parviflora albida—D 2290, T 736
C. rupicola—D 2277, DD 4288, T 1656, T 2608
Cerastium arvense—D 2240, T 744
Claytonia lanceolata—D 2141 (yellow form), D 2142, T 3149, T 3151 (yellow form)
Deschampsia atropurpurea—D 2266, T 764, T 1923
Draba incerta—DD 4264, T 4321
D. lonchocarpa—DD 4250b, DD 4254b, DD 4267b, DD 4272, T 1282, T 1657, T 1658, T 3529
D. paysonii trealeasii—DD 4347, T 1650, T 3144
D. praealta—D 2284, DD 4250a, DD 4254a, DD 4267a, DD 4350, T 1649, T 2583
D. stenoloba—DD 4248, T 3123
D. ventosa ruaxes—D 2280
Empetrum nigrum—T 3125
Epilobium alpinum clavatum—DD 4371
E. alpinum lactiflorum—DD 2257, T 1654
E. latiflolium—T 729
Eriogonum umbellatum subalpinum—D 2295
E. umbellatum hausknechtii—T 2182

[2] Collection was made by Tony Basabe, graduate student, Western Washington University.

TABLE 2. (Continued)

Erigeron compositus glabratus—D 2250, DD 4348, T 732, T 1266
E. peregrinus callianthemus scaposus—D 2287, DD 4274
E. peregrinus peregrinus peregrinus—DD 4376
Festuca ovina brevifolia—D 2248, T 765, T 1272
Gentiana glauca—D 2348, DD 4306, T 1232
Haplopappus lyallii—D 2243, T 741, T 1267, T 2592
Hieracium gracile—D 2297, T 3133
Juncus drummondii subtriflorus—D 2260, T 2599
J. parryi—D 2293, T 772
Lomatium martendalii—D 2300, T 748
Luetkea pectinata—D 2292, T 3127
Lupinus latifolius subalpinus—D 2256, T 3141
L. lepidus lobbii—D 2272, T 1223, T 2603
Luzula piperi—D 2261, D 2269, T 1235
L. spicata—DD 4278, T 3533
Lycopodium alpinum—D 2337
Mimulus tilingii caespitosa—T 2591
Oxytropis campestris gracillis—T 734, T 3137
Oxyria digyna—T 2605
Penstemon davidsonii menziesii—T 708, T 730, T 1221
P. procerus tolmiei—D 2263, D 2288, T 1217
Phacelia heterophylla pseudohispida—D 2258
P. sericea sericea—T 1269, T 1647
Phleum alpinum—T 758, T 1278
Phlox diffusa longistylis—T 755
Phyllodoce empetriformis—T 3143
Phyllodoce glanduliflora—T 1229
Poa alpina—D 2247, DD 4251, DD 4269, T 1276, T 2580, T 2597
P. cusickii epilis—D 2255, D 2304, DD 4377, T 762, T 763, T 2588
P. cusickii purpurescens—D 2267
P. gracillima—T 1273, T 1275, T 1279, T 1906, T 2581
P. incurva—T 2611
P. lepticoma paucispicula—T 1653, T 2598
P. rupicola—DD 4152, T 762, T 763, T 1968
P. sandbergii—D 2252, D 2281, DD 4353, T 1644
Polygonum bistortoides—T 3130
P. viviparum—D 2334, T 737, T 1665
Potentilla diversifolia diversifolia—D 2279, DD 4258, DD 4273, T 1228, T 3132
P. flabellifolia—D 2264, T 1177, T 1230
P. fruticosa—D 2254, T 740
P. villosa parvifolia—D 2282, DD 4311, T 1655
Polemonium elegans—T 1646
Ranunculus eschscholtzii eschscholtzii—DD 4369
Salix cascadensis—D 2329, D 2332, D 2333, D 2335, D 2338, T 1660, T 1661, T 3487, T 3488, T 3489
S. nivalis saximontana—D 2336, DD 4308, T 3490
Saxifraga bronchialis austromontana—D 2299, T 746
S. caespitosa emarginata—T 3528
S. debilis—DD 4365, DD 4366
S. ferruginea macounii, T 749
S. lyallii—DD 4367
Saxifraga occidentalis occidentalis—D 2301, DD 4263, T 3527
S. odontoloma—DD 4344
S. oppositifolia—DD 4247
S. punctata cascadensis—DD 4368, T 1664
S. tolmiei tolmiei—D 2259, T 739, T 1234
Sedum divergens—D 2302, T 3128
S. lanceolatum lanceolatum—D 2249, D 2286, T 747, T 1645
S. roseum integrifolium—D 2273, T 1651
Selaginella densa—T 2183
Senecio elmeri—DD 4225, T 1271
Sibbaldia procumbens—D 2303, T 1636
Silene acaulis escapa—D 2285, T 733, T 1224, T 1263
S. parryi—D 2291, D 2298, DD 4354, T 745, T 3131
Sitanion hystrix hystrix—D 2283, T 2185
Smelowskia ovalis—T 1652
Solidago multiradiata scopulorum—D 2238, T 3140
Stellaria longipes altocaulis—DD 4280, T 3530

TABLE 2. (Continued)

Taraxacum ceratophorum—D 2253, DD 4226, T 2586
Trisetum spicatum—D 2246, D 2268, T 757
Vaccinium caespitosum—DD 4246
V. deliciosum—T 1239, T 1637
V. occidentale—DD 4361
V. scoparium—D 2349
Veronica cusickii—D 2406, T 742, T 1220

[a] Chowder Ridge area includes Chowder Ridge and the adjacent northwest-southeast section of Skyline Divide.

Specimens are maintained in the herbaria of Western Washington University, Bellingham, Washington; University of Alberta, Edmonton, Alberta; or G. W. and G. G. Douglas, Victoria, British Columbia. Specimens are cited by collector (D = Douglas, DD = Douglas & Douglas, T = Taylor) and collector number. Nomenclature follows Hitchcock and Cronquist (1973).

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Stuart E. Nixon

Department of Zoology
Arizona State University
Tempe, Arizona 85281

Freshwater Triclads (Turbellaria) of Washington

Abstract

During a survey of freshwater habitats in Washington state, three genera of triclad flatworms (*Polycelis, Dugesia,* and *Phagocata*) were observed in such diverse environments as springs, streams, lakes, caves, and temporary ponds. Field data which included the temperature, pH and elevation of collection sites indicated that 1) *Polycelis* was restricted to relatively cold habitats such as springs and small montane streams; 2) *Dugesia* was common in lowland lakes and larger streams with more variable temperatures; and 3) *Phagocata* was found at a single locality, a temporary pond which was present for only three months of the year. The relationship between these ecological differences and the different life history strategies exhibited by these genera is discussed.

Introduction

Systematic statewide studies of freshwater flatworms in North America have added much to the understanding of this rather widespread and ecologically diverse group of aquatic organisms. In particular the work in Virginia (Kenk, 1935), Michigan (Kenk, 1944), Alaska (Kenk, 1953), Tennessee (Darlington and Chandler, 1972), and New Mexico (Chandler and Darlington, 1975) has increased our knowledge of the distribution and natural history of triclads greatly. No such systematic study has been undertaken in any of the states of the Pacific Northwest, and this report is an attempt to provide information of this nature from Washington and present comparative data from a wide range of freshwater habitats.

Methods and Materials

This survey was conducted throughout Washington state during 1973 and 1974, and as many types of freshwater environments as possible were examined. Thirty-three collection sites from fourteen Washington counties were included in the study, and the temperature and pH of the habitats were recorded at most sites. Flatworm collections were carried out for 30 minutes at each site and the number of individuals collected can be used to approximate relative population sizes. When utilizing these measures of relative frequency in comparisons between populations of different species, considerable error may be introduced because of differences in substrate preference. However, this type of behavioral variation is probably minimal within species except in cases of extreme environmental dichotomy such as between cave and epigean streams (see Nixon, 1974).

Following species identification of the collected specimens, microscopic observations were made in order to ascertain the frequency of sexual maturity in the populations. The term "mature" for each species listed below includes all individuals possessing reproductive organs, regardless of the degree of development. Use of this term should not imply that all individuals in this category were involved in sexual reproduction nor

that sexual reproduction occurs necessarily in populations containing mature individuals, for as Kenk (1973a) has pointed out in the case of *Polycelis*, although sexually mature individuals have been observed from many localities at different seasons, no egg capsules or cocoons have ever been observed in the North American species.

Results

Polycelis coronata (Girard)

This species was first described fully by Hyman (1931) from South Dakota, and subsequently has been reported from Colorado (Kenk, 1952), Alaska (Kenk, 1953; Holmquist, 1967), Utah (Beck, 1954; Braithwaite, 1962; Carpenter, 1969), Oregon (Hyman, 1963; Kenk, 1973a), Alberta (Ball and Fernando, 1968), New Mexico (Kenk, 1973a; Chandler and Darlington, 1975), and Montana, Wyoming, and Idaho (Kenk, 1973a). In 1937, D. M. Pike collected specimens of *Polycelis* from Mt. Rainier National Park, Washington, and Hyman deposited them in the National Museum of Natural History, Smithsonian Institution, under the name *P. coronata* (Kenk, 1973a).

Throughout its range, this species has been shown to be restricted to springs and streams of relatively low temperatures, and this finding was also characteristic of the species in this study. Specimens collected in Washington were observed in habitats ranging from 5 to 14 C which were at elevations of 76 to 1920 meters (250-6300 ft). The localities where pH was measured yielded values between 5.0 and 7.4. Five populations contained sexually mature individuals, and those localities exhibited considerably more narrow ranges in these aspects: temperature 10-11 C, pH 6.5-6.8, elevation 91-488 meters (300-1600 ft). Although mature individuals were collected from June through September, no conclusions can be made involving seasonal variation in this regard because many locations were inaccessible during winter months. The collection sites and field data from each site are listed below.

WHATCOM COUNTY

—spring in Bellingham, 51 individuals collected, 3 mature, 6/11/74, pH 6.5, temperature 11.0C, elevation 91 meters (300 ft).

—small stream near Sehome Hill, Bellingham, 3 collected, none mature, 5/21/74, 12.0C, 76 meters (250 ft).

—small stream on Lake Louise Road near Lake Whatcom, 4 collected, none mature, 5/23/74, 10.0C, 107 meters (350 ft).

—small stream near Lake Whatcom in Bellingham, 2 collected, none mature, 5/14/74, 13.0C, 91 meters (300 ft).

—small stream near Mt. Baker, 24 km (15 miles) east of Glacier, 43 collected, none mature, 9/21/74, pH 6.3, 5.0C, 1402 meters (4600 ft).

—small stream near Glacier Creek on Road 3409, 57 collected, 2 mature, 9/21/74, pH 6.8, 10.0C, 488 meters (1600 ft).

SKAGIT COUNTY

—small stream near Rt. 20, 29 km (18 miles) northeast of Marblemount, 76 collected, none mature, 9/28/74, pH 7.0, 12.0C, 305 meters (1000 ft).

—small stream near Old Cascade Highway, 4.8 km (3 miles) southeast of Marblemount, 62 collected, 2 mature, 9/28/74, pH 6.7, 10.0C, 183 meters (600 ft).

SNOHOMISH COUNTY

—small stream on Mt. Pilchuk, 5 collected, none mature, 8/29/74, pH 6.5, 7.0C, 1463 meters (4800 ft).

—small stream 4.8 km (3 miles) west of Monte Cristo, 211 collected, none mature, 8/29/74, pH 6.8, 9.0C, 732 meters (2400 ft).

—small stream 25.7 km (16 miles) southeast of Darlington, just east of Road 322, 108 collected, 6 mature, 8/29/74, pH 6.8, 10.0C, 427 meters (1400 ft).

—small stream near Big Four Ice Caves, 42 collected, none mature, 8/29/74, pH 6.5, 6.0C, 488 meters (1600 ft).

KING COUNTY

—small stream just east of SR 410, 12.8 km (8 miles) southeast of Enumclaw, 39 collected, none mature, 8/9/74, pH 7.0, 11.0C, 457 meters (1500 ft).

—creek just east of U.S. 2, 8 km (5 miles) west of Stevens Pass, 44 collected, none mature, 8/24/74, pH 6.2, 8.0C, 732 meters (2400 ft).

PIERCE COUNTY

—small stream 4.8 km (3 miles) northeast of Mt. Rainier, 25 collected, none mature, 8/9/74, pH 6.6, 9.0C, 1920 meters (6300 ft).

LEWIS COUNTY

—small stream 17.7 km (11 miles) northeast of Packwood, just east of SR 123, 64 collected, none mature, 8/9/74, pH 7.1, 11.0C, 640 meters (2100 ft).

SKAMANIA COUNTY

—small stream near Pimlico Creek, just north of SR 1302, 71 collected, none mature, 8/10/74, pH 6.4, 9.0C, 823 meters (2700 ft).

—small pool of water near spring in Deadhorse Cave, 21 collected, none mature, 8/10/74, pH 5.0, 6.0C, 884 meters (2900 ft).

—small stream near Swift Creek Resevoir, just south of Mt. St. Helens, 32 collected, none mature, 7/7/74, pH 6.9, 10.0C, 488 meters (1600 ft).

KLICKITAT COUNTY

—small stream just west of Road N84, 4.8 km (3 miles) north of Troutlake, 41 collected, none mature, 8/10/74, pH 6.8, 11.0C, 732 meters (2400 ft).

—small stream just west of Road N88, 3.2 km (2 miles) northwest of Troutlake, 6 collected, none mature, 7/7/74, 8.0C, 579 meters (1900 ft).

YAKIMA COUNTY

—small stream near Bird Creek, just east of Road N80, 14.5 km (9 miles) northeast of Troutlake, 45 collected, none mature, 7/6/74, pH 7.0, 10.0C, 1372 meters (4500 ft).

CHELAN COUNTY

—Bridge Creek, 14.5 km (9 miles) southwest of Leavenworth, 54 collected, none mature, 8/25/74, pH 7.4, 14.0C, 610 meters (2000 ft).

—small stream 16 km (10 miles) southwest of Leavenworth, 3 collected, none mature, 8/25/74, pH 7.1, 9.0 C, 671 meters (2200 ft).

SPOKANE COUNTY

—Big Springs on Mt. Spokane, 48 collected, none mature, 8/24/74, pH 6.5, 6.0C, 1250 meters (4100 ft).

CLALLAM COUNTY

—small stream 25.7 km (16 miles) south of Pt. Angeles, 46 collected, none mature, 8/16/74, pH 6.4, 8.0C, 1554 meters (5100 ft).

JEFFERSON COUNTY

—small stream near Hoh River Visitor Center, 51.5 km (32 miles) southeast of Forks, 86 collected, 4 mature, 8/16/74, pH 6.6, 11.0C, 183 meters (600 ft).

—small stream near Dosewallups Falls, 40.2 km (25 miles) southwest of Quilicene, 53 collected, none mature, 8/17/74, pH 6.8, 9.0C, 457 meters (1500 ft).

Dugesia tigrina (Girard)

This species along with *D. dorotocephala* is the most common and widespread triclad found in North America (Kenk, 1972) and has been reported from many types of freshwater habitats. Hyman (1963) noted the occurrence of both *Dugesia* species in Oregon, but failed to point out if they were found in the same streams and also made no mention of relative abundance. While being common in North America generally (occurring from coast to coast), this species is not nearly as common in Washington, having been found at only four localities. These habitats are considerably warmer than those of *Polycelis* and were all at relatively low elevations. The collection sites of *Dugesia* were:

WHATCOM COUNTY
—Lake Whatcom, 16 collected, none mature, 9/17/74, 17C, 91 meters (300 ft).
—Whatcom Creek (flowing from Lake Whatcom), 23 collected, none mature, 9/17/74, 18C, 91 meters (300 ft).
—Lake Fazon, 48 collected, 6 mature, 9/18/74, 15C, 76 meters (250 ft).

KITSAP COUNTY
—Long Lake, 46 collected, none mature, 8/30/74.

Unlike *Polycelis,* the *Dugesia* populations were observed in habitats with relatively slow water movement. Individuals of *Dugesia* were usually found on the aquatic vegetation in the lakes and were rarely observed on or under stones, whereas in Whatcom Creek most individuals were collected from the undersides of the larger rocks present. This behavior contrasted with that of *Polycelis* individuals which were found exclusively on the undersides of stones, possibly reflecting differences in rates of water flow.

Phagocata sp.

This triclad was found at a single locality in Bellingham, Whatcom County, a temporary pond which was present for only three months of the year. This pond was formed by heavy rainfall and melting snow during April of 1974 and 1975 and became dry by June of each year. Individuals of various sizes (3 to 10 mm) and colors (white, pink, tan) appeared soon after formation of the pond and were very abundant (hundreds of individuals observed) but extremely variable. Reproduction by fragmentation was observed as the pond began to warm and dry, similar to the processes reported in *Phagocata velata* (Stringer, 1909; Castle, 1928; Castle and Hyman, 1934; Kenk, 1944, 1972) and *P. vernalis* (Kenk, 1944, 1972). Further details of this process and illustrations of the Washington forms have been presented elsewhere (Nixon, 1977).

Sphalloplana sp.

A collection of specimens probably belonging to this genus has been made by C. M. Senger in a pool in Deadhorse Cave, Skamania County, during 1975 and 1976 (R. Kenk, pers. comm.). This is the same locality where partially cave-adapted specimens of *Polycelis* have been collected (Nixon, 1975, and this report). Like many cave-adapted forms, the *Sphalloplana* are white, eyeless planarians (Senger, pers. comm.), probably having lost pigmentation through regressive evolutionary processes.

Dendrocoelopsis vaginata Hyman

While not collected by the author in this study, this species has been recorded by Kenk (1973b) from Nigger Creek, Whitman County. Although Kenk does not mention the co-occurrence of this species with other triclads at this locality, B. Z. Lang observed (pers. comm.) that *Dendrocoelopsis, Polycelis, Phagocata* and *Dugesia* coexist in many springs and streams in seven eastern Washington counties. Specifically, Lang has recorded *Polycelis coronata, Phagocata oregonensis* and *Dendrocoelopsis vaginata* at the following localities:

WHITMAN COUNTY
—numerous springs at north end of Rock Lake.

SPOKANE COUNTY
—spring in city of Cheney.
—spring and brook below Pine Lake.

ADAMS COUNTY
—spring and brook 8 km (5 miles) north of Washtucna.

In addition, Lang noted that *Dendrocoelopsis vaginata* and *Dugesia sp.* were found in a creek in Spokane County, 8.8 km (5.5 miles) north of Reardan. He also collected *Dendrocoelopsis vaginata* and *Polycelis coronata* together at a spring west of Spring Lakes in Lincoln County. Although I recorded virtually no instances of coexistence of freshwater triclads in western Washington, such coexistence is common in eastern Washington. The causes of this difference are extremely puzzling, and elucidation of environmental factors involved in the dichotomy would be a worthy topic for future ecological research.

Discussion

The question of sexuality in natural populations of triclad flatworms is extremely complex, and the factors involved in inducing sexual maturity are probably different in each species. Indeed, differences among populations of a single species may vary in this regard. Kenk (1972:22) indicated that in *Dugesia dorotocephala* some populations may rely completely upon asexual reproduction but in others sexual reproduction may prevail. This may be the case in the Washington populations of *D. tigrina* as well, seeing that in one Whatcom County population sexually mature individuals were observed while in another none were observed.

In Washington populations of *Polycelis*, sexually mature individuals were relatively rare in most cases, and no egg capsules or cocoons were observed. Kenk (1973a) noted that no capsules or cocoons have ever been observed in any of the North American species of *Polycelis* and that the factors involved in inducing sexuality are unknown. The effect of temperature on sexual maturity and other aspects of the life cycle in European triclads has been shown by various workers (Reynoldson, 1960; Reynoldson *et al.*, 1965; Taylor and Reynoldson, 1962) and may also be important in North American species. Indirect evidence regarding temperature may be seen in the Washington populations of *Polycelis* which were observed in habitats between 5 and 14C. However, in the 28 populations studied, sexually mature individuals were observed only in those habitats between 10 and 11C, a relatively narrow temperature range.

In the *Phagocata* population studied in Whatcom County, sexually mature individuals were never observed; reliance upon the asexual process of fragmentation may be caused by the short time period available during the year.

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Gwilym S. Jones
John O. Whitaker, Jr.
Department of Life Sciences
Indiana State University
Terre Haute, Indiana 47809
and
Chris Maser[1]
Puget Sound Museum of Natural History
University of Puget Sound
Tacoma, Washington 98416

Food Habits of Jumping Mice (Zapus trinotatus and Z. princeps) in Western North America

Abstract

Major foods of 69 western jumping mice, *Zapus princeps*, and 93 Pacific jumping mice, *Z. trinotatus*, were generally similar to those of meadow jumping mice, *Z. hudsonius*. Seeds, particularly grass seeds, and fruits, such as of *Rubus* and *Vaccinium*, were important, as was the fungus *Endogone*. Animal matter was less abundant than in *Z. hudsonius*, but the chief animal food in *Z. princeps* and *Z. trinotatus* was lepidopterous larva as in *Z. hudsonius*.

Introduction

Detailed studies have been presented of the food habits of jumping mice, *Zapus hudsonius* and *Napeaozapus insignis* from New York (Whitaker, 1963a, 1963b) and *Z. hudsonius* from Indiana (Whitaker and Mumford, 1971). There is scant information, however, concerning the foods of the western or Pacific jumping mice, *Z. princeps* or *Z. trinotatus*, although several papers refer in general terms to their diets. Some of these papers are cited here. Maser and Franklin (1974) stated that thimbleberry *(Rubus parviflorus)*, salmonberry *(R. spectabilis)*, evergreen huckleberry *(Vaccinium ovatum)*, skunk cabbage *(Lysichitum americanum)*, seeds, moss, and fungi were foods of *Z. trinotatus* in Oregon, and Maser (unpublished) found that blueleaf huckleberry *(Vaccinium deliciosum)*, Himalayan blackberry *(Rubus procerus)*, and stinking current *(Ribes bracteosum)* were utilized as foods in Oregon. Dalquest (1948) listed velvet grass *(Holcus lanatus)*, grass seeds, dock *(Rumex)*, skunk cabbage, and blackberries as foods of this species in Washington. Clark (1971) presented a general analysis of the foods of *Z. princeps* from Teton County, Wyoming. He found "seeds" to comprise the greatest quantity of the diet (82 percent volume, 100 percent frequency) followed by green vegetation and arthropods in trace amounts. Bailey (1930) found only "clean white starch" in *Z. princeps* which he examined from Yellowstone Park, Wyoming. Grass seeds were reported as foods by Armstrong (1972), Ingles (1965), Henshaw and Birdseye (1911), and Banfield (1974) from several localities. Banfield (1974) listed "summer berries." Whitaker (1962) reported small percentages of *Endogone* from the stomachs of *Z. princeps* from California, and Dowding (1955) reported *Endogone pulvinata* from this species in Alberta, Canada.

[1] Present address: Range and Wildlife Habitat Laboratory, Route 2, Box 2315, La Grande, Oregon 97850.

The purpose of this paper is to present information on the food habits of *Z. trinotatus* and *Z. princeps* from western North America.

Methods and Materials

Jumping mice for this study were collected during two trips into western North America by Gwilym S. and Diana B. Jones in the summers of 1973 and 1974, and by Chris Maser during his work on mammals of the Oregon Coast (1970-1973). Stomach contents were examined with a 10 to 70 power, zoom dissecting microscope. Identifications were made by comparison with known items. Stomachs from *Zapus princeps* were examined from the following localities: British Columbia (26 stomachs, most from near Quesnel), Wyoming (21, most from Albany and Carbon Counties), California (11 from Nevada County), and Utah (11, most from Weber County). Stomachs from *Zapus trinotatus* were examined from the following localities: Oregon (43, from several counties), British Columbia (27, most from the Fraser River Valley near Hope), Washington (20, most from Mason County), and California (3 from Humboldt County).

Results and Discussion

Results of stomach analysis are presented for *Zapus trinotatus* (Table 1) and *Z. princeps* (Table 2). For comparison, some of the major foods of *Z. hudsonius* from New York (Whitaker, 1963a) were summarized. Since most of the present collections were in summer, *Z. hudsonius* data for July, August, and September were used, including 159, 138, and 191 stomachs respectively. Percentage volumes of major groups of foods for those months were grass seeds 36.4, 26.9, 30.8; other seeds 21.7, 28.5, and 23.3; *Endogone* 16.7, 15.1, 19.5; lepidopterous larvae 5.6, 6.5, 8.4; other animal foods 1.3, 2.1, 2.8; and fleshy fruits *(Fragaria, Vaccinium, Rubus,* and *Viburnum)* 4.6, 7.6, and 5.7.

There are great similarities between the food habits of eastern and western jumping mice. Seeds, particularly grass seeds, are the predominant food. Seed content in the stomachs of *Z. trinotatus* ranged from 49.6 to 56.6 percent of the total volume, and in *Z. princeps* it ranged from 28.8 to 52.3 percent. These are similar to the values from New York (54.1 to 58.1 percent). Grass seeds ranged from 33.8 to 46.7 in *Z. trinotatus,* 9.5 to 62.1 in *Z. princeps* and 26.9 to 36.4 in *Z. hudsonius.*

The second major group of foods eaten by North American zapodids consists of subterranean fungi, particularly *Endogone. Endogone* ranged from 5.5 to 19.9 percent volume in *Z. trinotatus,* 1.4 to 17.7 in *Z. princeps,* and 15.1 to 19.5 in *Z. hudsonius.* Odors emitted by the maturing sporocarps allow the mice to detect and dig out the hypogeous fungi. In eastern *Z. hudsonius, Endogone* is usually found in greater abundance in individuals from more moist situations. (Whitaker, 1962, 1963a), but we have too little information to determine the relationship of this food to habitat of western or Pacific *Zapus.*

Animal materials, chiefly lepidopterous larva, were eaten at rates of 6.9, 8.6, and 11.2 percent in the summer by *Z. hudsonius.* Animal materials were utilized slightly less in this sample of *Z. trinotatus,* with values ranging from 3.5 to 6.3 percent volume. In *Z. princeps* from British Columbia and Wyoming, animal foods totaled only 0.8 and 3.8 percent of the volume respectively. However, in those from California and Utah they were 13.7 and 45.1 respectively. Local abundance of larvae and other insects probably influenced the values in these small samples.

TABLE 1. Food from 43 stomachs of *Zapus trinotatus* from Oregon, 3 from California, 20 from Washington, and 27 from British Columbia.

	Oregon & California		British Columbia		Washington	
	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Grass seeds	37.5	73.9	46.7	92.6	33.8	90.0
Rubus spectabilis Salmonberry	15.0	28.3	0.1	3.7	10.4	35.0
Unidentified seeds	10.5	23.9	2.9	11.1	5.1	40.0
Starchy material	9.3	13.0	3.7	3.7	—	—
Endogone	6.1	30.4	5.5	51.9	19.9	70.0
Lepidopterous larvae	5.0	45.7	4.0	18.5	2.5	20.0
Vaccinium parviflorum Red Huckleberry	3.9	6.5	—	—	1.5	5.0
Cerastium seeds	3.5	10.9	trace	7.4	17.6	60.0
Unidentified vegetation	3.1	28.3	3.9	44.0	5.0	55.5
Unidentified fungi	1.7	15.2	trace	3.7	2.8	20.0
Lonicera involucrata Twinberry	1.5	2.2	1.8	22.2	—	—
Unidentified insect	1.0	19.6	0.4	18.5	0.8	20.0
Gaultheria shallon seeds Salal	0.8	6.5	—	—	0.1	5.0
Rubus sp.	0.4	2.2	—	—	0.1	5.0
Formicidae	0.2	4.3	—	—	—	—
Unidentified animal	0.1	2.2	—	—	0.2	10.0
Rumex seeds	0.1	4.3	trace	3.7	—	—
Aphididae	trace	2.2	trace	3.7	—	—
Moss	—	—	0.2	3.7	0.5	5.0
Rubus parviflorus Thimbleberry	—	—	30.6	59.3	—	—
Mites	—	—	0.1	7.4	—	—
Coleoptera	—	—	trace	3.7	—	—
	99.7	.	99.9	.	100.3	.

The last major category of foods eaten by zapodids is that of the fleshy fruits, such as those of *Vaccinium* or *Rubus*. Fruits, heavily utilized by North American zapodids, are likely preferred over many types of foods, as they are generally consumed when available. Some fruits are available for only a short period, but may form a major proportion of the diet at that time. The kinds of fruit vary. In the east, major fruits are the strawberry *(Fragaria virginiana)*, the various blackberries and raspberries (*Rubus* spp.), the blueberries (*Vaccinium* spp.), and the fruit of arrowwood *(Viburnum dentatum)*. In the west, the fruits of *Rubus* and *Vaccinium* are again eaten, particularly salmonberry *(R. spectabilis)*, thimbleberry *(R. parviflorus)*, and red huckleberry *(Vaccinium parviflorum)*. Salmonberry was the major food in a series of stomachs examined from *Z. princeps* from British Columbia, and also in *Z. trinotatus* from Oregon, California, and Washington. *Vaccinium* and other fruit presently unidentified were also important. Fruit of thimbleberry (actually mostly seeds in this case) was important in the *Z. trinotatus* sample from British Columbia. The fruits of both salmonberry and thimbleberry fall to the ground when mature and are readily available to the mice. The mice obtain some berries, such as those of salal *(Gaultheria shallon)*, by climbing into the low bushes.

Food habits of North American mice of the genus *Zapus* are similar in that the various species feed on the same four major groups of foods. The group listed in

approximate order of decreasing use are: seeds, particularly grass seeds, subterranean fungi of the genus *Endogone*, animal materials, particularly lepidopterous larvae, and fleshy fruits, varying with locality.

TABLE 2. Food from 26 stomachs of *Zapus princeps* from British Columbia, 11 from California, 21 from Wyoming, and 11 from Utah.

	British Columbia		California		Wyoming		Utah	
	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Rubus spectabilis Salmonberry	27.8	42.3	—	—	—	—	—	—
Grass seeds	23.1	50.0	45.9	54.5	62.1	80.1	9.5	18.2
Endogone	12.9	46.2	17.7	54.5	9.1	28.6	1.4	9.1
Vaccinium	10.4	23.1	—	—	0.7	4.8	—	—
Unidentified vegetation	9.8	53.9	5.0	27.3	5.2	38.1	2.7	18.2
Unidentified fruit	8.7	19.2	—	—	—	—	—	—
Unidentified seeds	5.6	19.2	6.4	36.4	6.1	23.8	41.4	90.9
Unidentified fungi	1.0	3.8	5.5	9.1	2.9	9.5	—	—
Lepidopterous larvae	0.6	7.7	10.0	27.3	0.5	4.8	42.3	81.8
Scarabaeidae	0.2	3.8	—	—	—	—	0.9	9.1
Cerastium seeds	0.1	3.8	—	—	5.5	14.3	—	—
Starchy material	—	—	5.0	18.2	4.5	4.8	—	—
Unidentified insect	—	—	2.3	27.3	1.2	9.5	0.5	9.1
Carabidae	—	—	1.4	9.1	—	—	—	—
Rubus sp.	—	—	0.9	9.1	—	—	—	—
Coleoptera	—	—	—	—	1.4	4.8	—	—
Diptera	—	—	—	—	0.7	4.8	—	—
Chrysomelid larvae	—	—	—	—	—	—	0.9	9.1
Formicidae	—	—	—	—	—	—	0.5	9.1
TOTAL	100.2		100.1		99.9		100.1	

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W. H. Rickard

and

R. E. Fitzner

Ecosystems Department
Battelle Northwest Laboratories
Richland, Washington 99352

Avifaunal Survey of the Trojan Nuclear Power Station[1]

Abstract

A walking path was established that entered or passed the important bird habitats present on the undeveloped property surrounding the Trojan Nuclear Power Station in Oregon. Ten early morning walks were made at approximately one month intervals in 1973. All identifiable birds were counted. Seventy-eight species were recorded from the path. If faithfully conducted over a period of years, the bird path method of avifaunal censusing can be expected to detect at least gross changes in bird populations as related to changing land use patterns.

Introduction

The National Environmental Policy Act (NEPA) of 1969 has created a need for providing written statements to evaluate the environmental impacts of construction and operation of nuclear power stations and other kinds of industrial facilities. Birds usually inhabit sites potentially suitable for nuclear power stations and are an important consideration because certain species are regarded as rare, threatened, or endangered. Others are commercially and recreationally valuable.

One of the important questions is: How much of an effort needs to be made to comply fully with the intent of NEPA? Probably the most extensive effort made towards evaluating impact assessments so far is that associated with nuclear power station siting and the United States Nuclear Regulatory Commission (Eberhardt, 1976).

This paper reports the results of an avifaunal survey made prior to the operation of the Trojan nuclear power station.

The Site

The Trojan nuclear power station is located on a 600-acre site near Prescott, Columbia County, Oregon. The land is mostly undeveloped and is occupied by forest communities. The forests are interrupted by small hay meadows, freshwater ponds, and grassy marshes. The dominant trees are Douglas-fir, *Pseudotsuga menziesii,* growing on the upland soils; and black cottonwood, *Populus trichocarpa,* and Oregon ash, *Fraxinus latifolia,* growing on lowland soils.

Methods

Prior experience as to the kind of information and detail needed to provide data to assess the long-term impact of power station operations on bird populations was lack-

[1] This study was funded by the Portland General Electric Company, Portland, Oregon.

ing. Thus, an arbitrary decision was made to establish a survey path to be followed once each month and to record all birds seen along this path. The path was walked in the early morning hours and was approximately 2.5 miles long (Fig. 1). The path penetrated conifer forest and deciduous tree communities, skirted the edges of marsh

Figure 1. Aerial photograph of the Trojan nuclear power station. The dotted line shows the bird survey path. The path begins at the upper (northern) property boundary and terminates near the prominent cooling tower structure. The rectangular reflection pond west of the cooling tower is approximately 1500 feet in length. (PNL 766-075-1)

and pond habitats, and forest and meadow edges. When in forest stands, the line of sight was often restricted to a few yards, but in open areas line of sight would extend to ½ mile or more.

An aerial photograph (Fig. 1) was taken to provide a record of the extent of plant communities and to serve as an indicator of future changes in communities, such as clear-cut logging or other events that could alter the species composition and relative abundance of birds along the path. In all, 10 visits were made at about 1-month intervals.

Bird identifications were made with the aid of binoculars, but it was not always possible to identify all birds seen, especially those in heavy cover. Unidentified birds were not included in the species lists.

Results

Upland game birds were not abundant at the Trojan site even though five species were represented (Table 1). Birds reared on the site property can easily cross boundaries where they could be shot during the hunting season even though hunting is not permitted on the site property.

TABLE 1. Birds counted along an established survey path at the Trojan Power Station Site, 1973.

Common Name	J	F*	M	A	M	J	J	A	S	O	N*	D
Upland Game Birds												
Ruffed Grouse									1			1
Mountain Quail								9	7			
Mourning Dove							2					
Ring-necked Pheasant										1		
Band-tailed Pigeon							2					
Waterfowl												
Mallard Duck			11	10	10	3	16	15	18	~200		21
Wood Duck					6		1		1			
American Coot	1									10		29
American Wigeon	75		45									
Canada Goose	50											42
American Merganser	9		2									
Hooded Merganser					10							
Green-winged Teal										13		
Pintail										2		
Hawks and Vultures												
Red-tailed Hawk	2		1	4		2	2	1	1			1
Turkey Vulture				1				1				
Gulls and Shorebirds												
Great Blue Heron	2		1	3	10	8	3	17	2	4		1
Killdeer			2	2		3	1	1	1	12		
Spotted Sandpiper					3	4	2	2				
Ring-billed Gull	~240				2							
Western Sandpiper								3				
Lesser Yellowlegs								2				
Herring Gull				10								
Black-crowned Night Heron								2				
Perching Birds												
Black-capped Chickadee	8		10	12	2	6	2	10	10	29		15
Song Sparrow	15		8	7	10	6	8	8	22	13		17
Robin			8	2	8	3	4	4	4	5		1
Steller's Jay	1		5	1	4	2	2	3				7
Red-winged Blackbird			1	10	15	10	5		~150	10		3
Winter Wren	1		3	4	2	1		4		9		3
Rufous-sided Towhee	1		1	2	2	3	6					4
Dark-eyed Junco	40		6	1	2			6				57

TABLE 1. (Continued)

American Goldfinch		2	10	10	15	~100			
Purple Finch				3	8	2	2	4	
Common Flicker	2		1		2	1	1		
Chestnut-backed Chickadee			1		6	14		26	2
Rough-winged Swallow			6	6	6	~100	∞		
Barn Swallow			20	9	8	60	∞		
Long-billed Marsh Wren		4	2					2	4
Common Crow		3	2	2				1	
Starling			1	15	8		4		
White-crowned Sparrow	1				5	6	1		
Common Bushtit		1	1		1	1			
Violet-green Swallow				12	8	60	∞		
Pine Siskin			4		8	10			
Yellowthroat		3	2	1					
Hermit Thrush				6	2	1			
Bewick's Wren		2		4	4				
Brown-headed Cowbird			4	10	18				
Ruby-crowned Kinglet	2			1				1	1
Northern Oriole				4	4	4			
Golden-crowned Kinglet				3				21	54
Orange-crowned Warbler		2	1		2				
Hammond's Flycatcher			2	1	4				
Olive-sided Flycatcher			2		3	1			
Downy Woodpecker							1		1
Cliff Swallow			20	8					
Tree Swallow		8	30						
Cedar Waxwing				1	2				
annah Sparrow					16	2			
ack-headed Grosbeak				3	3				
Rufous Hummingbird		2			1				
Western Tanager					2		1		
Hutton's Vireo							1		1
Alder Flycatcher				4	2				
Trail's Flycatcher		3	4						
Hairy Woodpecker						2	1		
Warbling Vireo		1							
Black-throated Gray Warbler						3			
Yellow-rumped Warbler		8							
Yellow-bellied Sapsucker				1					
Williamson's Sapsucker								1	
Brewer's Blackbird							1		
House Finch									1
Varied Thrush									2
Brown Creeper								4	
White-throated Sparrow								1	
Fox Sparrow									5

Birds observed on the site but not along the established pathway: Pied-billed Grebe, Whistling Swan, Cinnamon Teal, Blue-winged Teal, Ring-necked Duck, Goshawk, American Kestrel, Common Snipe, Great Horned Owl, Calliope Hummingbird, Belted Kingfisher, Pileated Woodpecker, Western Wood Pewee, Bank Swallow, Purple Martin, Scrubjay, Water Pipit, Yellow Warbler, MacGillivray's Warbler, Wilson's Warbler, and House Sparrow.

*=No observations made

Ducks and geese were much more numerous than upland game birds, especially in the autumn months when migrant birds fed and rested on the ponds. The species recorded during this season were similar to those reported on public shooting grounds on Sauvie Island (Oregon Dept. of Fish and Wildlife, 1975). The ponds were not great producers of ducks, although a few broods of mallards and wood ducks were raised (Table 1). Mallards and wood ducks are reported as the principal nesting ducks in Columbia County (Oregon Dept. of Fish and Wildlife, 1975).

Predatory birds were scarce. The most often sighted raptor was the red-tailed hawk (Table 1). The great blue heron was abundant, having been seen on every visit, and 17 individuals were counted during one survey. These birds do not nest on the Trojan property, but a large nesting colony is reported from Bachelor Island located in the Columbia River upstream from the Trojan property.

The diversity of habitats at the Trojan site is mainly responsible for the variety of bird species. Seventy-eight species were recorded from the census path and twenty-one additional species were identified during the course of other biological studies on the site property (Table 1).

There were no rare, threatened, or endangered species observed during the course of field observations, although the whistling swan is protected from hunting kills in Oregon (U.S. Dept. of Interior, 1973; Marshall, 1969).

Discussion

The purpose of avian surveys at nuclear power station sites is to establish whether rare, threatened, or endangered species occur on the property and, if so, to determine if their existence would be threatened by construction and operation of the site. Another purpose is to determine if common, commercially, or recreationally valuable bird populations would be seriously affected by construction and operation of the station.

Nuclear power stations, like other kinds of massive building complexes, pre-empt natural avian habitats. Unlike many other kinds of industrial complexes, nuclear power stations are sited with a large buffer zone of undeveloped land around the buildings. The acreage varies, but 1,000 acres is probably fairly representative. The land use in the buffer zone varies according to site, but human residences are not permitted.

Depending on future land use priorities, the buffer zone lands can provide habitat for birds for the life of the nuclear station, *i.e.*, 30-40 years, in a zone in which wildlife habitats could dwindle with the development of housing, agriculture, or other industrial facilities.

The anticipated proliferation of nuclear power stations in the United States has increased public concern as to the deleterious potential for nuclear power station operation on wild bird populations, and this concern has prompted Mellinger and Schultz (1975) to review the literature involving wild birds and ionizing radiation. The normal operation of a modern nuclear power station is expected to release only small amounts of radionuclides into the surrounding atmosphere. Low level atmospheric releases are expected to produce ecological effects that would be inseparable from those produced by an array of concomitant environmental stresses. Some bird mortality may result from collisions with buildings, towers, and other structures such as transmission lines. This kind of mortality can be ascertained by observing if dead birds are

found at the bases of the structures. To date, there has been no bird mortality as a result from collisions with buildings, the cooling tower, or other man-made structures on the Trojan site. Eberhardt (1976) reviewed environmental statements prepared for 15 nuclear stations in the United States in terms of their contributions to quantitative ecological methods and concluded that the limitations of animal census methods and substantial variability make it doubtful that anything less than gross population changes can be detected in the usual sequence of pre- and post-operational ecological observations.

The bird path survey has some advantages over the plot census technique as employed by Anderson (1973). It is less time-consuming and permits coverage of more habitats. The bird path survey is expected to detect at least gross changes in species composition and abundance. The major disadvantage is that population density (*i.e.,* individuals per unit area) is not obtainable. Density data are essential if comparison between different habitats and regions is to be made, but they are not so important if each nuclear power station site is treated individually.

A bird path survey was conducted on a riparian tree-shrub community in south-central Washington and seemed to assess adequately changes in avian populations after a 10-year time lapse (Rickard and Rickard, 1972).

Although bird populations are more amenable to census methodologies than most other kinds of wild vertebrates, and considerable time and effort have been expended to elucidate ecological principles in northwestern forest communities (e.g., Wiens and Nussbaum, 1975; Anderson, 1972), the bird path census appears adequate for nuclear power plant impact assessment, particularly if done faithfully, frequently, and in conjunction with knowledge of changing plant community patterns as indicated by changing land uses and on-going radiological surveillance programs.

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James R. Habeck

Department of Botany
University of Montana
Missoula, Montana 59801

A Study of Climax Western Redcedar (Thuja plicata Donn.) Forest Communities in the Selway-Bitterroot Wilderness, Idaho

Abstract

Old-growth *Thuja plicata* forest communities occurring in the Selway-Bitterroot Wilderness in northern Idaho were the subject of investigation. It is within this wilderness that western redcedar reaches its southeastern range limits in Idaho. Mature, climax cedar groves sampled in both lower and upper drainage segments indicate that only the stands at higher elevations are reproducing themselves at this time. Lower cedar groves have well-developed overstories, but lack reproduction. The lower cedar groves may be experiencing stress in consequence of lower moisture at its range limits and are incapable of reproducing successfully. A hypothesis is presented that high wildlife populations in the past depleted the cedar reproduction, and this depletion effectively inhibited vegetative propagation of the redcedar.

Introduction

Some of northern Idaho's most spectacular, surviving examples of old-growth western redcedar *(Thuja plicata)* groves and other old-growth forest composed of redcedar and grand fir *(Abies grandis)* exist within the central portion of the half-million hectare (1.2 million acres) Selway-Bitterroot Wilderness (46° 00′ N, 115° 00′ W, Fig. 1). Redcedar grove communities, 400 to 500 years old, are common on the streamside flats and lower terraces of Moose Creek, Bear Creek, and other tributaries of the upper Selway River.

Very little scientific study has been made of these particular wilderness forests. Although the entire Selway-Bitterroot Wilderness is well within the designed "core area" reportedly investigated by Daubenmire (1952) and by Daubenmire and Daubenmire (1968, see their Fig. 1), it has become apparent that very little, if any, of the roadless wilderness portion of their study area was in fact examined or data collections made (Daubenmire and Daubenmire, 1968, Appendix B: stand locations) in this wilderness. Current vegetation studies, partially reported here, have been pursued during a five-summer period between 1971 and 1975.

By omitting data collection within this part of northern Idaho, the Daubenmires (1968) failed to give recognition to several special phenomena that occur in the Selway-Bitterroot Wilderness particularly associated with redcedar-grand fir communities. It is within this wilderness portion of Idaho that *Thuja plicata* reaches its southeastern range limits. It has been noted in these current studies that as redcedar approaches its range limits, its ecological behavior and competitive interactions with its close associate, grand fir, are altered. In some portions of the wilderness old-aged redcedar stands are showing no evidence of reproducing themselves, whereas elsewhere the cedar is reproducing very successfully.

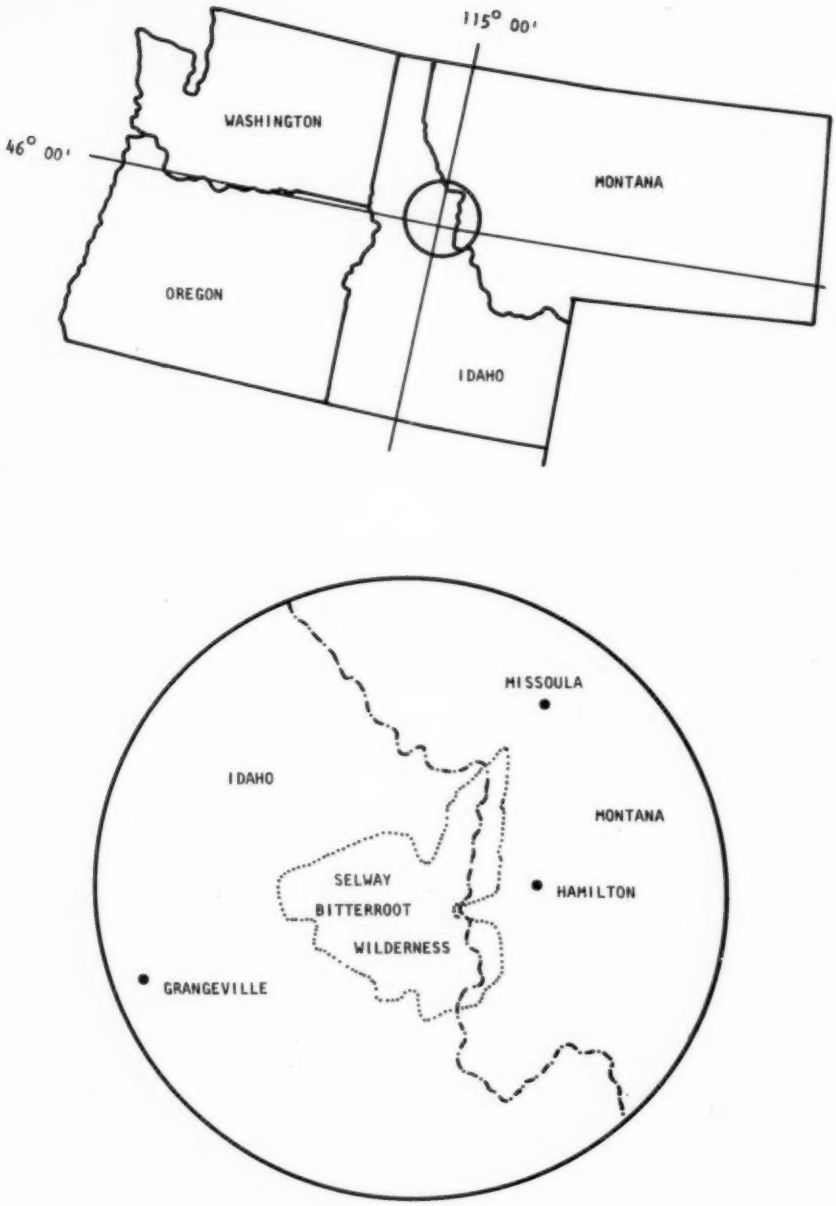

Figure 1. Location Maps of the Selway-Bitterroot Wilderness in northern Idaho.

It is the objective of this paper to present field data collected from a series of old-growth redcedar-grand fir communities that will provide an insight into the current status of climax *Thuja plicata* forests within this part of the cedar's botanical range. An interpretation of these data should contribute to a better understanding of the problems that have been experienced in applying habitat type classification developed by the Daubenmires (1968) to redcedar-grand fir communities in this portion of their core area (Steele, Arno, and Pfister, 1976).

Phytogeographical Features

Daubenmire has described and discussed in detail the occurrence of Pacific Coastal floristic elements in northern Idaho (1943, 1952, 1969). In addition, Little (1971) has provided a detailed atlas of Pacific Northwest tree distributions, and the eastward extensions into northern Idaho of such species as western redcedar, grand fir, western whitepine *(Pinus monticola)*, western hemlock *(Tsuga heterophylla)*, western yew *(Taxus brevifolia)* and others are well documented. The available literature on tree distribution patterns in northern Idaho clearly reveals that the Selway-Bitterroot Wilderness lies within a key phytogeographical zone.

It is within the region bounded by the Lochsa River to the north and the Salmon-Clearwater River divide to the south that several of the major coastal tree species reach their southeastern range limits. Western larch and western whitepine both occur just within the northern edge of the wilderness but exist only as scattered small populations or isolated individuals. Redcedar is common along the major stream courses within the northern half of the wilderness but becomes less common farther south; it reaches its southern limits in the vicinity of the upper reaches of the Selway River. Western hemlock, a common associate of redcedar north of the Lochsa River, has not been seen within the wilderness.

Grand fir, in contrast, extends well southward from the wilderness, and reaches its range limits in portions of central Idaho. With other coastal species reaching their range limits, grand fir exhibits an expansive distribution in the wilderness area and adjacent parts of the Nezperce National Forest. Grand fir without question is the most widely distributed species on the Selway River drainage; it occupies warm aspects at elevations below 600 m, mingling with formerly fire-maintained ponderosa pine *(Pinus ponderosa)* savannahs, as well as forming mixtures with subalpine fir *(Abies lasiocarpa)* and Engelmann spruce *(Picea engelmannii)* at elevations up to 1,800 m. As a consequence of grand fir's behavior, a Douglas-fir *(Pseudotsuga menziesii)* forest zone is poorly and incompletely developed within much of the wilderness.

Description of the Study Area

Detailed destriptions of the basic geography, geology, and climatic features of the Selway-Bitterroot Wilderness have been published elsewhere (Leiberg, 1900; Lindgren, 1904; Habeck, 1972, 1976; Greenwood and Morrison, 1973; Finklin, 1974). In general, the wilderness is characterized by steep, mountainous terrain, with local relief between streamsides and ridgetops often 1000 to 1500 m. The highest elevations (about 3000 m) occur on the eastern boundary (Bitterroot Mountains), while the lowest altitudes (about 550 m) are found on the northwestern corner along the lower Lochsa River.

Annual moisture is well correlated with an east-west gradient, with local modifica-

tions induced by the terrain features. Western areas receive about 900 mm per year, and the upper slopes of the Bitterroot Mountains receive 1500 mm annually, much of it in the form of snow. Summer (July-August) temperatures at highest elevations average 16C, lower areas 22C; January temperatures range from –8C in the eastern mountains, to –2C in the lower western section of the wilderness.

The July-August period is typically warm and dry; it is during this period that summer lightning storms are common and the cause of wildfire ignitions (Habeck, 1972, 1976). Past fires have burned streamside redcedar-grand fir forests, but not with the same frequency as upland forests. Only rarely has it been noted that fires on adjacent upland slopes have spread into the moist cedar groves. Lightning often causes ignitions within the groves, but generally these have not led to widespread burning within the groves.

Since catastrophic wildfire occurs so infrequently in the streamside cedar forests, time allows the development of stands that are four or more centuries old. It is these climax forests that are given particular attention in this report.

Methods

The study of old-growth red-cedar fir forests in the Selway-Bitterroot Wilderness has been a part of a larger fire ecology study (Habeck, 1976) wherein stand samples were taken within all forest zones, and form a wide variety of successional stands in each zone. Forest stand structure in these studies was documented by utilizing a reconnaissance plot technique as described by Steele *et al.* (1975). Communities selected for structural and compositional characterization were examined closely and a 375 m^2 circular plot was positioned in a location considered typical for the entire stand. Within this plot all trees over 1.4 m in height were tallied by diameter size classes. Trees less than 1.4 m in height were tallied within a central 50 m^2 subplot; these tree counts were then converted to numbers per 375 m^2.

An estimate was made of the canopy coverage (Daubenmire, 1959) for each tree species, in each of three diameter classes, *viz.*, over 3 dm dbh, 1-3 dm dbh and under 1 dm dbh. Seven coverage classes were employed: T = 0-1 percent, 1 = 1-5 percent, 2 = 5-25 percent, 3 = 25-50 percent, 4 = 50-75 percent, 5 = 75-95 percent, and 6 = 95-100 percent. In calculating average cover percentages, the mid-points were used, *viz.*, 0.5 percent, 3.0 percent, 15.0 percent, 37.5 percent, 62.5 percent, 85.0 percent, and 97.5 percent.

The vascular understory species within the 375 m^2 plots were also assigned coverage values using the same scale used for the trees. Shrubs, ferns, and other forbs observed within the stand, but not occurring within it, were separately recorded as present. The nomenclature used follows Hitchcock and Cronquist (1973).

Stand aging did not prove to be a simple matter. Both *Thuja plicata* and *Abies grandis* exhibit decay within the heartwood (species of *Poria* and *Fomes* on redcedar, and *Echinodontium tinctorium* on grand fir). Heart rot destroys the inner growth rings, making precise aging impossible. An estimated age was extrapolated by counting rings within the sound wood, and then relating these to total stem diameter.

Results

In the course of sampling, a total of 84 stands were examined in detail. These occupy sites that range in elevation from 618 m to 1690 m (2040 to 5590 ft.). Stand ages

range from 22 to approximately 600 years. Only those stands over 300 years of age are considered here. Stands of this age support only a few surviving seral species, mostly Douglas-fir and ponderosa pine. The stand structure of these old-growth forests involves redcedar and grand fir, and a comparison of the two species was a major objective of this study.

One of the most clear-cut influences on cedar population dynamics involves elevation. By simply hiking elevational transects along stream courses, one is impressed by the gradual shift that takes place in the reproductive success of redcedar. At elevations below 1000 m, cedar appears to be doing very poorly, whereas at altitudes above 1000 m, within the same drainage system, the redcedar is reproducing itself as successfully as observed anywhere else in northern Idaho or northwestern Montana.

The basic nature of this elevational shift can be interpreted readily from the data summarized in Tables 1 and 2. In Table 1, a representative group of old-growth communities occurring at elevations below 870 m are summarized; Table 2 provides a similar compilation for a group of stands occurring at elevations above 1100 m.

The common feature seen in the stands existing at lower drainage positions is the absence of redcedar reproduction (trees smaller than 1 dm dbh) even though a well-developed overstory of cedar exists in each case. Grand fir is generally well represented in these lower stands, with stand 11 an exception. Grand fir does not display the longevity or have the ultimate growth potential of redcedar, and finding grand firs over 8 dm dbh is a rare event. None of the redcedar stands sampled by the Daubenmires

TABLE 1. Tree population analysis for a series of lower drainage cedar stands. The number of individuals of *Thuja plicata* (Thpl) and *Abies grandis* (Abgr) occurring within 375 m^2 plots is presented, distributed within diameter size classes.

Stand No. Stand Age Elevation	Species	Seedlings Below 1.4 m ht.	Diameter Classes (dm at dbh), Trees Over 1.4 m ht.									
			0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	>10
6	Thpl			2		1		1			1		
450 yrs	Abgr		6	12	3		2		1	1	1		2
690 m													
11	Thpl												5
600 yrs	Abgr				3								
717 m													
14	Thpl			1	3		3	3	1	2			
315 yrs	Abgr	45	6	4	4	1			1	1			
717 m													
19	Thpl			2	5	2	1		1	6	2		
400 yrs	Abgr	15	4	3	9	5							
733 m													
56	Thpl							1	4	2			
350 yrs	Abgr	60	3	4	2	2	1	1					
760 m													
20	Thpl				3	3		4	2	3		2	
420 yrs	Abgr	56	10	6									
760 m													
17	Thpl			1	2			2	1		2		1
450 yrs	Abgr	23	11	4	3	1	2	1					
780 m													

TABLE 2. Tree population analysis for a series of upper drainage cedar stands. The data are arranged as in Table 1.

Stand No. Stand Age Elevation	Species	Seedlings Below 1.4 m ht.	Diameter Classes (dm at dbh), Trees Over 1.4 m ht.									
			0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	>10
180 325 yrs 1106 m	Thpl	29	17	5	2	2	1			1			
	Abgr	37	5										
51 500 yrs 1133 m	Thpl	127	5	4	1		1	1					1
	Abgr	175	6	4	2	2				2			1
23 500 yrs 1140 m	Thpl	45	9			2	1		2	1		2	3
	Abgr	15	4										
24 475 yrs 1150 m	Thpl	97	7	1	2	1	1					1	2
	Abgr									1	1		
50 425 yrs 1150 m	Thpl	440	21	5	2	2	2	5	1		1		
	Abgr	172	15										
57 400 yrs 1217 m	Thpl	180	11	2	2	1	1		2	3			
	Abgr	32	3	1	1								
121 385 yrs 1480 m	Thpl	22	6	2	2	2		2	1	1			
	Abgr	15	1	5			1			1			

(1968, p. 63, *Thuja/Pachistima* habitat type) display this sort of population structure, and only one out of ten of their old-aged stands shows a similar sort of reproductive failure by redcedar.

In contrast, the climax redcedar forests occurring in upper drainage sites above 1000 m (Table 2) exhibit excellent reproductive success. Grand fir is present in all stands, and it also is reproducing successfully in most of these cedar stands. It is these higher stands that show a greater degree of similarity to the stands sampled by the Daubenmires (1968); it may be significant that nearly all of their samples of this community type occur at elevations over 1000 m.

The differences in reproductive success of redcedar in lower and upper drainage sites within the Selway-Bitterroot Wilderness are further emphasized in the data summarized for 29 climax stands in Table 3. Here average canopy cover percentages for redcedar and grand fir within three diameter size classes are provided. There are only minor differences in the average canopy cover among old, larger redcedars over 3 dm dbh in upper and lower drainage positions. The higher cedar communities, however, have cover values that are three times larger for intermediate-size trees (1-3 dm dbh), and about 40 times greater cover for cedar reproduction in the smallest diameter class.

Canopy coverage of grand fir is generally greater among the lower drainage stands, considering the mature trees only; it can be determined from the data in Tables 1 and 2 that the average number of grand fir reaching or exceeding diameters of 3 dm dbh is greater among the low elevation communities. Grand fir reproduction, however, is

TABLE 3. Comparison of average cover percentages, by diameter size classes, for *Thuja plicata* and *Abies grandis* occurring within two series of old-growth, streamside stands. Group A below occur below 1000 m, and have an average age of 430 years; group B occur above 1000 m and average 445 years.

Species: Diameter Size Classes		Cover Percentages Group A (n=14)	Group B (n=15)
Thuja plicata:	Over 3 dm dbh	55.7%	53.2%
	1-3 dm dbh	4.1	14.2
	Under 1 dm dbh	0.6	24.7
Abies grandis:	Over 3 dm dbh	10.8%	2.4%
	1-3 dm dbh	16.4	6.0
	Under 1 dm dbh	5.7	11.7

more dense at higher elevations.

Table 4 provides a list of the major understory species encountered in the 14 plot samples included in Tables 1 and 2. Cover class values are entered in this table, and it is evident that many of the understory plants have similar levels of occurrence and ranges of variation from plot to plot in both upper and lower stand groups. Among the 28 species listed, only *Clintonia uniflora* and *Coptis occidentalis* are found in all stands; they also have rather consistently high cover values. None of the 14 plots support all of the species; stand 121 has the lowest diversity (16 species), while stand 57 exhibits 24 of the species listed.

Eight of the understory species appear to have differential distribution patterns between the two stand groups. *Lonicera ciliosa* and *Spiraea betulifolia* are confined to lower drainage sites; *Menziesia ferruginea, Taxus brevifolia, Xerophyllum tenax, Athyrium filix-femina, Gymnocarpium dryopteris* and *Pyrola asarifolia* show a preference for higher drainage sites.

Perhaps because the forest communities being discussed here occur at or near the range limits of *Thuja plicata,* difficulties are experienced when an attempt is made to apply the Daubenmires' (1968) habitat typing classification to the stands summarized in Tables 1-4. Although the stands in Table 1, at lower drainage stations, might comprise exceptional cases, one is obligated to classify these stands as *Abies grandis-Pachistima* habitat types, since the redcedar is not reproducing itself. The stands listed in Table 2 represent a mixture of interactions between redcedar and grand fir; redcedar is reproducing itself well in all cases, but grand fir shows continuous reproduction in only a few, moderate regeneration in several others, and no reproduction in one of the stands. All of these stands would likely be classified as either *Thuja-Pachistima* habitat types or *Thuja-Athyrium* habitat types.

The fundamental basis for the Daubenmires' classification system is founded on their belief that within a given habitat, one tree species is competitively superior to all others, and an analysis of population structure will provide evidence of the tree species that will achieve monospecific dominance. However, even the Daubenmires (1968, p. 29, p. 55) recognize that this line of reasoning does not fit redcedar and grand fir interrelationships in Idaho. They state that grand fir is but "slightly less successful" than redcedar, and is usually not eliminated between destructive wildfires in the redcedar habitat types. The Daubenmires also describe the role of grand fir as "almost climax" in these habitat types.

TABLE 4. Cover class values for a group of common understory species found in the stands listed in Tables 1 and 2. Cover classes defined in text. + = present in stand, but not in plot.

Species	Lower Drainage Stands									Upper Drainage Stands				
	6	11	14	19	56	20	17	180	51	23	24	50	57	121
Shrubs:														
Amelanchier alnifolia	T		T	1	T	T	T	T	T	T		T	+	
Lonicera ciliosa	T				T	1	T							
Lonicera utahensis	T			1	T	T	T	T		T		T	2	T
Rhamnus purshiana	T	T		T	T	T	T		T	+	1	T	+	
Menziesia ferruginea				2				T	T		T	T	T	+
Spiraea betulifolia				1	T	1	T							
Rosa gymnocarpa	1	T	T	3	T	2	T	T	T	+	T	T		
Taxus brevifolia			+					3	2	2	3	1	2	2
Vaccinium globulare			1	2	T	1	T	T	2	1		1	+	3
Linnaea borealis			3	5	2	5	T	2	3	1		2	1	
Ferns:														
Adiantum pedatum	T	4	+		T		2			2	1			
Athyrium filix-femina		4	T	+					T	1	3		T	+
Gymnocarpium dryopteris		T	T						+	4	3		T	
Forbs:														
Adenocaulon bicolor	2	1	3	1	1	3	2	T	T	2	2		+	T
Asarum caudatum	2	2			+	1	3	1		3	3	T	T	+
Chimaphila umbellata				T	T	T		T	3			2	1	2
Clintonia uniflora	2	T	2	3	3	4	1	2	3	1	1	2	2	1
Coptis occidentalis	4	1	4	4	3	4	4	4	3	2	3	3	3	3
Cornus canadensis	T	T	1	2		2	2	2	1	1	T	1	2	
Circaea alpina		5				1	3			2	4			
Galium triflorum	1	2	1	2	1	2	1	T		2	1	T	2	
Goodyera oblongifolia	+		T	T	T	2	T	T		+	T	T	T	T
Osmorhiza chilensis	1	T	T	1	T	1	1		T	1	T	T	T	+
Pyrola asarifolia			T					T	1	+			T	1
Smilacina stellata	T		1	2	1	2	1	2		3	2	1	1	
Tiarella trifoliata	1	2	2	3	1	3	2		1	2	T	T	T	+
Trillium ovatum	T	+	T	1		2	1	T	1	1	2	T	T	T
Xerophyllum tenax									1			T	T	+

Observations and field data collected in the Selway-Bitterroot Wilderness support the view that a gradational shift exists between grand fir-dominated forests on better drained slopes to redcedar-dominated communities on moist streamside sites. Communities exhibiting shared dominance also exist. It is probably only to serve utilitarian purposes (forest management) that it would be justified to classify these cedar-grand fir forests arbitrarily into discrete habitat types, and avoid any effort to establish a separation based on natural discontinuities that do not appear to exist.

Discussion

The ecological behavior of *Thuja plicata* appears to be altered in some portions of the Selway-Bitterroot Wilderness, based on the data presented. Of major significance is the evident reduction or loss of reproductive redcedar capacity at lower elevations on the Selway River drainage system. The old-growth cedar stands at elevations below 1000 m have not successfully established reproduction for many years, and even trees up to 1 dm dbh are very rare. In these same lower drainage stands, *Abies grandis* is doing very well.

The reverse appears true for redcedar at higher elevations. Observations in upper drainage stands, above 1000 m, indicate a relatively healthy situation for redcedar. In many cases the redcedar reproductive layer is so dense that foot travel is difficult. Close examination of this cedar reproduction reveals that much of it has originated from vegetation propagation, and not sexual reproduction. This finding is identical to observations made on cedar regeneration in old-growth stands further north in Idaho, as well as in Glacier Park in northwestern Montana (Habeck, 1958). Seedlings originating from seed do not appear highly tolerant to dense shade.

It might be speculated that redcedar is not establishing itself well at lower elevations because conditions for vegetative reproduction are absent or limiting. Cedar limbs torn from trees by windstorm or snow are capable of producing adventitious roots if a moist microsite is available and remains moist during the summer. A majority of the cedar saplings examined at higher sites originate, however, from intact, lower limbs that touch the soil surface, or from small trees that are tipped over by heavy snowpacks.

If snow accumulations are higher and longer lasting at upper elevations and not so at lower sites, this difference might explain the situation discussed in this paper. To explain the data in Table 1 on this basis, one has to suggest that recent climatic modifications have taken place, leading to recent reductions in snowpacks. There is no evidence that this event has happened, however. Lower drainage positions seem to receive sufficient snow and total annual moisture to support cedar growth. Trail right-of-ways through the lower cedar groves, where sunlight penetrates to the ground layers, do support sexual seedling reproduction in small amounts.

There is another possible explanation for the lack of cedar reproduction at lower elevations; it includes a combination of events involving historical wildfire and past elk and deer populations in the Selway River drainage. Large fires occurring between 1910 and the mid-1930s created thousands of acres of seral brushfields (Giles and Snyder, 1971; Young and Robinette, 1939). The abundance of food and the remoteness of the area fostered the development of unusually high elk and deer populations. If the lower elevation cedar communities functioned to any degree as winter range,

a great pressure could have been exerted on any available winter food. It is possible that the small-sized cedars in the lower groves were simply destroyed by wintering elk and deer. Such a loss would have curtailed the most effective means the cedar has to reproduce itself in old-growth stands. Thus a major gap could have been created in the population structure of these lower groves, and the impact still remains today.

Within the Selway-Bitterroot Wilderness, *Thuja plicata* is responding to a deterioration of the Pacific maritime influence, and this response is likely the major reason it reaches its range limits in this region. If one believed that the range of redcedar was actually shrinking northward and westward, it would be expected that such a range reduction would first appear among the lower elevation populations; one could perhaps document that the cedar was not reproducing well on marginal sites (low elevations), but was continuing to do well where moisture was higher (upper elevations). The destructive influence of high numbers of elk and deer could then be interpreted as simply speeding up an inevitable reduction of the redcedar populations at lower sites.

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